The interrelations of action perception and action production across the life span

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Zusammenfassung

Soziale Interaktionen basieren auf der Vorwegnahme des Verhaltens Anderer. Durch diese Antizipation der Handlungsziele unserer Interaktionspartner können wir unser eigenes Handeln dem ihrigen anpassen. Bisherige Forschung hat gezeigt, dass diese Wahrnehmung von Handlungen anderer Personen und die eigene Handlungsausführung eng zusammenhängen. Ausserdem verändern sich im Laufe des Lebens sowohl Wahrnehmung als auch Ausführung. Die vorliegende Dissertation untersucht, ob sich auch das Zusammenspiel von Handlungswahrnehmung und -ausführung über die Lebensspanne unterscheidet.

Innerhalb von drei Studien wurde mittels Eyetracking und behavioralen Massen die Handlungswahrnehmung und –ausführung von Personen zwischen 3 und 80 Jahren (Studie I) und 20 und 80 Jahren (Studie II und Studie III) erfasst. Die Ergebnisse zeigen keine Unterschiede zwischen den Altersgruppen im verzögerten Einfluss von Wahrnehmung auf Ausführung über die Lebensspanne. Im Gegensatz dazu nahmen die unmittelbaren Einflüsse von Wahrnehmung und Ausführung aufeinander mit fortschreitendem Alter zu. Handlungswahrnehmung und -ausführung waren zudem von der akkumulierten motorischen Erfahrung und der motorischen Kompetenz der Probanden beeinflusst. Zusammengefasst zeigen die vorliegenden Ergebnisse Variabilität und Stabilität über die Lebensspanne im Zusammenhang von Handlungswahrnehmung und –ausführung in Abhängigkeit individueller Merkmale der handelnden/ wahrnehmenden Personen.

Abstract

Social interaction requires the anticipation of our interlocutors' behaviour. Through this anticipation we are able to adjust our actions to our counterparts' intentions and implicit goals. The ability to anticipate others' action goals is based on a tight coupling between our perception of actions and our action production ability. However, action perception and production undergo life-long developmental change and so might their coupling. Therefore, this thesis aims at describing the life span trajectory of the interrelations of action perception and production.

Using eye-tracking technology and behavioural measures, action perception and production of participants between 3 and 80 years were assessed within three consecutive cross-sectional studies. Results indicate a relatively stable deferred influence of perception on production across the life span. In contrast, the immediate influences within the coupling were accentuated towards late adulthood. Furthermore, these age-related differences were influenced by the participants' accumulated action experience across the life span and their motor competence. Taken together, the findings of this thesis show stability and variability in the action perception-production coupling across the life span in relation to (age-dependent) individual characteristics.

„Im Anfang war die Tat!“ (Goethe, 1808, Vers 1237)

Contents

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Abbreviations

AOI	Area of interest
AON	Action-observation network
EEG	Electroencephalography
fMRI	Functional magnetic resonance imaging
MEP	Motor-evoked potentials
RT	Reaction time
RQA	Recurrence quantification analysis
TMS	Transcranial magnetic stimulation

Part I

Introduction

Imagine being late for a train bringing you to a conference to which you were invited as a keynote speaker. You are running through a crowded train station, trying to beat the unforgivable clock. Another traveller is coming your way, the same grim expression on his face. You already see it coming. Not long before both of you are forced to stop, and in the middle of this crowded train station it begins, the inevitable dance. Who is going to pass to the left? Who takes the right side? Only after an endless series of awkward back-and-forth movements, half-hearted attempts to choose a side, and growing despair, you manage to pass each other and continue your journeys.

The ability to understand others' actions is a cornerstone of human culture (Rizzolatti & Craighero, 2004). From early on in life, we are able to perceive other people's actions as being directed toward goals rather than simply a combination of random movements (Woodward, 1998). Based on this understanding, we predict goals of actions – both while producing them ourselves as well as when observing others performing an action (Flanagan & Johansson, 2003). This active prediction of action goals allows us to prepare and adjust our answer to other people's behaviour and implicit and explicit goals (Blakemore & Decety, 2001), and fosters the correct interpretation of intentions (Gallese & Goldman, 1998; Iacoboni, 2005). Hence, it builds the basis for social interaction, cooperation, joint action, and social learning (Blandin, Lhuisset, & Proteau, 1999; Sebanz & Knoblich, 2009; Yon & Press, 2018).

According to previous work, the perception of our own and other people's actions (*action perception*) is based on overlapping processing structures for perceptual and motor information (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Prinz, 1990, 1997). Therefore, our action perception is largely informed by our ability to produce these actions (*action production*) and vice versa (Brass, Bekkering, & Prinz, 2001). Prior work also indicates that action perception and production undergo life-long developmental change (Diersch et al., 2013; Gampe, Prinz, & Daum, 2015). However, our knowledge is based on inferences of studies investigating selective age groups with varying methodologies. It is still unclear whether action perception and production follow similar developmental trajectories or whether their interrelation differs across development. That is, to date no study has taken the life-span perspective on the action perception-production coupling. Therefore, this thesis aims at describing the developmental trajectory of the interrelation of action perception and production across the life span – from childhood to late adulthood.

Before describing and discussing findings of three consecutive studies exploring this question, a short overview of the current state of research is given. This overview focuses on the life-span trajectories of action perception and production and provides relevant information to retrace the research gap this thesis aimed to fill. The following remarks are therefore incomplete with regard to other aspects of the action perception-production coupling such as a detailed description of theoretical approaches or measurement techniques. Hence, the next chapters are dedicated to three questions: Why are action perception and action production assumed to be interrelated in the first place? How does this coupling show up in behavioural and neural studies? And, how do action perception and action production vary across the life span?

1. Theoretical framework

The next two sections lay the basis for the subsequent review of empirical findings on the action perception-production coupling. The first section provides definitions and common operationalizations of perception and production. In the second section, different theoretical frameworks accounting for the interrelation of action perception and production are described and integrated.

1.1 Definitions and measures of action perception and production

Here, the terms *action*, *action production*, and *action perception* are defined and connected to measurement techniques and operationalizations used in previous work. For this thesis, *actions* are defined as goal-directed (complex) sequences of movements (Prinz, Beisert, & Herwig, 2013). Actions can be described on the goal, the kinematic and the muscle level (Grafton & Hamilton, 2007; Hamilton & Grafton, 2007). The goal level refers to the intention of the person acting (e.g., „I want to feel more awake.") or the physical action goal (e.g., coffee cup). Hence, action goals can either be abstract or concrete (Prinz, Beisert, & Herwig, 2013). For this thesis, only concrete action goals were used. On the kinematic level, the movement kinematics to reach the action goal are defined (e.g., the exact shape and trajectory of the hand grasping the cup). Finally, the muscle level incorporates the muscle activity patterns resulting in these kinematics.

1.1.1 Action production

The physical characteristics (i.e., speed and accuracy) of the execution of specific actions will be called *action production*. In previous research, action production has been measured in various ways. For example, it was assessed via the accuracy of action imitation (Casile & Giese, 2006; Gampe et al., 2015), the quality of action execution (e.g., how many fingers are used to grasp an object, Ambrosini et al., 2013), the speed of action initiation and execution (e.g., reaction times, Brass, Zysset, & Von Cramon, 2001), or (parental) report (e.g., children's crawling ability, van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008; self-reported ability to perform an action, Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012). For this thesis, action production was measured via the accuracy of imitation and the speed of action initiation and execution. In *Study I* participants were asked to imitate a previously observed multistep action. Their behaviour was coded manually and rated in terms of its closeness to the observed action. The resulting imitation score indicates how accurate the participants reproduced the action. In *Study II*, participants were asked to respond with a finger movement to pre-defined cues. The initiation and execution of this movement was assessed via participants' reaction times (latency between stimuli onset and participants' key press). The resulting reaction time served as an indicator of participants' action production given the observed cues.

1.1.2 Action perception

Action perception describes the processing of sensorimotor information about one's own and others' actions. That is, the perceiver interprets and predicts incoming information through a comparison to his or her knowledge base about actions (Gallahue, Ozmun, & Goodway, 2012). Similar to action production, action perception has previously been operationalized with different paradigms and measurement techniques. Some studies have used action-priming paradigms, in which the latency of participants' attention shifts in direction of hand or pointing actions is measured (Daum & Gredebäck, 2011; Daum, Ulber, & Gredebäck, 2013; Wronski & Daum, 2014). A second way, in which action perception has been assessed, is via participants' evaluation of actions. For instance, participants were asked to indicate others' walking speeds (Jacobs & Shiffrar, 2005), to judge their own action range (Gabbard & Caçola, 2011), or to detect biological movement patterns in point-light figures (Casile & Giese, 2006). In infants and children, increased looking time (Daum, Prinz, & Aschersleben, 2011; Woodward, 1998) or pupil dilatation (Gredebäck & Melinder, 2010) as a reaction to unexpected action events often served as an indicator of action evaluation. A third way in which action perception has been measured is via the (differences in the) activity of the sensorimotor system during action observation (Gangitano, Mottaghy, & Pascual-Leone, 2001; Gazzola & Keysers, 2009). Finally, another measure of action perception is the participants' anticipation of others actions (Flanagan & Johansson, 2003). In these studies, participants are asked to either predict the continuation of a partially occluded movement (Springer et al., 2011; Stadler et al., 2011; Stadler, Springer, Parkinson, & Prinz, 2012) or the latency of their anticipatory eye movements towards others' action goals was measured

(Flanagan & Johansson, 2003). Such anticipatory eye movements are present during the production as well as the perception of simple goal-directed actions in adults (Flanagan & Johansson, 2003) and infants (Rosander & von Hofsten, 2011). They have become an established indicator for action perception – especially in studies exploring its interrelation with action production (Falck-Ytter, Gredebäck, & von Hofsten, 2006; Gesierich, Bruzzo, Ottoboni, & Finos, 2008; Melzer, Prinz, & Daum, 2012).

For this thesis, action perception was measured via participants' anticipation of action goals (*Study I* and *Study III*) and the recurrence in their fixation sequences (*Study I*). For this purpose, participants' eye movements during action observation were assessed with an eye tracking system. The system used for the studies of this thesis (Eyelink 1000 Plus, SR Research) infers the coordinates of participants' gaze on a screen based on their eyes' cornea reflection of a near-infrared signal. Eye-tracking technology is non-invasive, does not require special preconditions, and is therefore particularly suitable for life-span research (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003). Specifically, eye tracking can be employed without giving participants explicit instructions, is flexible and adaptable to different research designs and robust to participants' bodily movements (Gredebäck, Johnson, & von Hofsten, 2010). To measure participants' anticipation of action goals, the arrival time of their gaze shifts at the action goal (indicated via *areas of interest*; AOIs) was compared to the agent's arrival time at the same area. If their gaze arrived in goal area before the agent did, this indicated anticipation of the goal of the particular action step. Participants' *anticipation frequency*, defined as the proportion of anticipated action steps per observed action steps, was used as an indicator of action perception. It quantifies the ability to anticipate the goal of the agent's action.

To explore participants' idiosyncratic gaze pattern, *recurrence quantification analysis* (Zbilut & Webber, 1992) was performed on their fixation behaviour. With this method, patterns within a nonlinear behavioural time-series may be identified (Zbilut & Webber, 1992). Recurrence quantification analyses (RQA) have been used previously to describe complex dynamic systems (e.g., climatological data: Marwan & Kurths, 2002; heart-rate variability: Marwan, Wessel, Meyerfeldt, & Schirdewan, 2002) and to analyse gaze patterns (Anderson, Anderson, Kingstone, & Bischof, 2015; Anderson, Bischof, Laidlaw, Risko, & Kingstone, 2013). For this thesis, participants' fixation sequences were analysed in terms of their recurrence. Two fixations were considered recurrent if they landed in the same AOI. Participants' fixation sequences were divided into equally long time intervals and for each interval it was assessed in which AOI participants' gaze was located at this point in time. This sequence was then mapped with itself over all time intervals to obtain the recurrence rate. The *recurrence rate* is defined as the percentage of recurrent fixations per fixation sequence. It indicates how often observers re-fixated previously fixated AOIs and informs about the stability of participants' action perception.

In sum, the preceding paragraphs illustrate the variability in paradigms and tasks used to measure action perception, production, and their coupling. The next section takes a theoretical standpoint on the interrelation between action perception and production and aims at answering the following question: Why are action perception and action production assumed to be interrelated?

1.2 Explaining the action perception-production coupling

Research has been concerned with the action perception-production coupling for the past 100 years (James, 1890; Piaget, 1952). Already early work on the human mind has emphasised the notion that action perception and production are interrelated (James, 1890). According to James (1890), there is no difference between the processing of perceived and produced actions and the mere thinking of actions and their effects has the capability to trigger and guide their execution. Also Piaget (1952) suggested that infants in their first two years begin to understand the world through the sensorimotor effects of their own bodily movements indicating an early interrelation of perceptual and motor information.

This and other work has been re-discovered by Prinz (1990, 1997), who formulated an explicit approach on the interrelation between action perception and production stating that „perceived events and planned actions share a common representational domain" (Prinz, 1997, p. 129). At the same time, reports on mirror neurons within the premotor cortex of macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) helped fostering scholars' interest in this field. Mirror neurons code for action perception and action production (Gallese et al., 1996). Hence, the very same neurons discharge during the macaques' action production as well as during their perception of others performing the same action. Meanwhile there is growing evidence of an equivalent system in humans (Rizzolatti & Craighero, 2004) and different theoretical frameworks explaining the perception-production coupling have been developed (for an overview see Pezzulo, Candidi, Dindo, & Barca, 2013). Among others, those frameworks include the ideomotor theory of action (Greenwald, 1970), predictive coding models (Friston, 2005), the common-coding approach (Hommel et al., 2001), and the simulation theory (Jeannerod, 2001).

The ideomotor theory of action (Greenwald, 1970; James, 1890) states that actions are processed in terms of their sensory consequences (e.g., tones, words, colours). Action perception and production are based on previous experience with one's own movements and their effects in the world. This results in a repeated coupling of a certain movement with the according sensory effects. The emerging association may then be activated by motor and sensory input and the mere expectation of an effect (for instance through action perception) is enough to initiate action production. In a similar vein, predictive coding models (Friston, 2005; Kilner, Friston, & Frith, 2007) assume that internal models of actions develop in response to experiences with actions and their consequences. The information within these models is then matched with the actual sensory effects and differences between the two are minimised through repeated feedback loops. Action perception is therefore based on the information within the perceiver's motor repertoire. This notion is also reflected in the assumptions of the common coding approach (Hommel et al., 2001). According to this approach, perceived and produced actions are based on a shared representational basis and common coordinative resources. That is, similar motor programmes to those needed to produce actions are activated during action perception and action planning (Gallese et al., 1996; Iacoboni et al., 1999; Léonard & Tremblay, 2008; Marty et al., 2015). Finally, the simulation theory (Jeannerod, 2001) states that, in addition to the overt and observable stage of action, there is another – covert – stage of action. This covert stage involves aspects of the future such as the goal of the action, the means to reach it, or the consequences of the action without an overt action production. Specifically, action production as well as action perception are assumed to automatically elicit an overt and real-time (Graf et al., 2007) simulation of the according action. This internal simulation is supported by a network involving the sensorimotor system (Valchev, Tidoni, Hamilton, Gazzola, & Avenanti, 2017).

The theoretical frameworks reviewed above take different perspectives on the action perception-production coupling. They vary in the exact mechanisms they assume to underlie the action perception-production coupling, in the features of actions that are proposed to be represented (e.g., distal features like speed/orientation or proximal features like the exact object on which is acted), and the level on which these processes are assumed to take place (e.g., individual neurons or neuronal networks). However, their propositions also share some core assumptions. (1) The reviewed frameworks imply shared processing resources within the sensorimotor system for action perception and production. (2) Additionally, they propose that actions are processed in an anticipatory manner. Specifically, actions are perceived and initiated in terms of the sensory effects they (were intended to) cause. (3) Finally, the frameworks indicate that the relation between action perception and action production is capable of changing over time, for example as a consequence of experience.

In line with the first assumption, research has shown that cortical areas activated during action perception overlap with areas involved in action production (Filimon, Nelson, Hagler, & Sereno, 2007; Munzert, Lorey, & Zentgraf, 2009). For instance, studies on the action-observation network (AON) show shared neural activation during action perception and production in a set of neuronal structures including sensorimotor and frontoparietal regions and the posterior superior temporal sulcus (Grafton, 2009; Stadler et al., 2011). In the same vein, studies using transcranial magnetic stimulation (TMS) during action perception have shown a modulation of the motor corticospinal excitability in accordance with the actions perceived (Aglioti, Cesari, Romani, & Urgesi, 2008; Buccino et al., 2001; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano et al., 2001; Urgesi, Moro, Candidi, & Aglioti, 2006; Valchev et al., 2017). Pertaining to the second assumption, Nyström (2008) found a desynchronisation of the mu-rhythm during the perception of goal-directed actions in infants and adults. This electroencephalography (EEG) rhythm is recorded over sensorimotor sites and its desynchronisation is associated with motor activity in infants, children, and adults (Bowman, Thorpe, Cannon, & Fox, 2017; Pfurtscheller, Neuper, Flotzinger, & Pregenzer, 1997; Southgate, Johnson, El Karoui, & Csibra, 2010). Strikingly, in Nyström's study, this desynchronisation peaked before the observed actor reached the goal. Therefore one may conclude that the sensorimotor system is involved in the anticipation of action goals (Rizzolatti, Fogassi, & Gallese, 2001). Finally, supporting the third assumption, studies looking at the cortical processing of actions in infants, adults, and older adults (Diersch et al., 2012; Nyström, 2008) have reported differences between the participants studied. This indicates developmental variations in the action perception-production coupling across the life span. In the next chapter, previous work on these age-related differences in action perception, production and their interrelation is reviewed.

2. Action perception and production across the life span

Action perception and production are shown to be interrelated from early on in ontogeny up to old age (Diersch, Jones, & Cross, 2016; Woodward, 1998). Furthermore, they undergo developmental changes across the life span (Diersch et al., 2016; Gampe et al., 2015). The following sections are dedicated to exploring the nature of these variations in infants, toddlers, young, and older adults.

2.1 Interrelation of action perception and production in infants and toddlers

Action perception and action production are shown to increase in accuracy and velocity across infancy and toddlerhood (Gampe et al., 2015; Sommerville & Woodward, 2005). Already in infancy, action perception and production are interrelated and action production abilities positively correlate with action perception abilities (Cannon, Woodward, Gredebäck, von Hofsten, & Turek, 2012; Daum et al., 2011; Gredebäck & Kochukhova, 2010; Longo & Bertenthal, 2006; Loucks & Sommerville, 2012). For instance, while simple reaching or feeding actions are already anticipated by 6-month-olds (Kochukhova & Gredebäck, 2010), only at the age of 12 months, infants anticipate the goal of more difficult reach-and-transport actions (Falck-Ytter et al., 2006). Infants at 6 to 10 months of age, who were better at performing a precision grasp, were also faster in anticipating other's precision grasping movements (Ambrosini et al., 2013). In the same vein, 12-month-olds ability to perform a contralateral reaching action was associated with their ability to anticipate the goal of such an action (Melzer et al., 2012). On the neural level, action production and perception elicit similar cortical responses in infants (Marshall, Young, & Meltzoff, 2011; Southgate, Johnson, Osborne, & Csibra, 2009) and the desynchronisation of the motor-related mu-rhythm during action perception is shown to vary with 9- and 12-months-old's quality of action production (Cannon et al., 2016; de Klerk, Johnson, Heyes, & Southgate, 2015; Yoo, Cannon, Thorpe, & Fox, 2016).

In sum, previous work suggests that action perception and production are tightly coupled during infancy and toddlerhood and show parallel developmental trajectories. Hence, infants' ability to produce an action is assumed to be a strong contributor to their perception of others' actions. However, there is also research not finding such a correlation between infants' action perception and production (Csibra, 2008; Daum, Prinz, & Aschersleben, 2009; Hernik & Southgate, 2012). Instead, the authors of these studies suggest that infants perceive and understand others' actions based on different cues such as the efficiency with which the action is performed (Gergely & Csibra, 2003), its self-propelledness, or the occurrence of an action-effect (Biro & Leslie, 2007). This has lead to a controversy in the field on whether action perception and production truly have a common basis and develop simultaneously. So far, a clear prospect on this issue has yet to be established. Furthermore, data on older children and adolescents is rare, which additionally prevents a coherent picture on the life-long trajectories of action perception and production. A recent exception to this (McKyton, Ben-Zion, & Zohary, 2017) points to a strong role of previous experience in concurrent perception and production in establishing a coupling between them. In this study, 12-year-olds, who had impaired vision for most of their lives and had just regained their sight, were compared with healthy controls. The newly sighted children showed a decreased coupling between action perception and production compared to the control children (McKyton et al., 2017).

In conclusion, a clear picture on the development of the action perception-production coupling across childhood has not been established yet. On the one hand, this might be due to the variance in tasks and methodologies employed. On the other hand, previous research mostly focussed on infants and toddlers, while older children have not been studied intensively yet.

2.2 Interrelation of action perception and production in young adults

In young adults (i.e., student samples aged 20 – 35 years), action perception and action production are shown to exert bi-directional influences on each other on various time scales. That is, one may observe immediate influences if perception and production are performed at the same time (e.g., Brass, Bekkering, Wohlschläger, & Prinz, 2000; Hamilton, Wolpert, & Frith, 2004) or one may observe a deferred influence from one on the other, for instance as a result of training or life-long experience (e.g., Capa, Marshall, & Bouquet, 2011; Hecht, Vogt, & Prinz, 2001).

One prominent example for the immediate effects of the perception-production coupling is the occurrence of interference and facilitation effects in simultaneous action perception and production. Previous research has shown that action perception is modulated by a concurrent action production (Hamilton et al., 2004; Kilner, Paulignan, & Blakemore, 2003). This may result in interference effects in cases in which the perceived and the produced action do not match. For instance, participants judged the gait speed of point-light walkers less accurately if they were walking themselves (in a different speed) compared to when they were standing or executing an unrelated movement (Jacobs & Shiffrar, 2005). In contrast, previous research has also shown that action perception can be facilitated by a congruent and simultaneously produced action (e.g., Miall et al., 2006). For example, participants were better at detecting a waving point-light arm in a scrambled mask if they were executing waving movements themselves (Christensen, Ilg, & Giese, 2011). Similar effects could be found for the influence of action perception on action production (Brass, Zysset, et al., 2001; Edwards, Humphreys, & Castiello, 2003; Ménoret, Curie, Portes, Nazir, & Paulignan, 2013; Wohlschläger & Bekkering, 2002). For instance, participants were shown to be faster opening their hand when observing someone else performing a similar hand-opening action than during the perception of a hand-closing action (Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000).

When looking at more deferred influences within the action perception-production coupling, studies indicate that already a short training in producing an action enhances the accuracy and speed of predicting the action goal (Casile & Giese, 2006; Hecht et al., 2001; Möller, Zimmer, & Aschersleben, 2015). For instance, training participants to respond with a closing-hand action to the perception of an opening-hand action results in the absence of the previously reported interference effects (Heyes et al., 2005) and alters the related sensorimotor processing (Catmur et al., 2008; Catmur, Walsh, & Heyes, 2007).

To sum up, the reviewed studies show that action perception and action production are interrelated during adulthood, observable in the immediate and deferred influences they elicit on each other. The reported findings also indicate variance across adults (e.g., as a result of training), which is related to differences in the activity patterns of the sensorimotor system. However, most of the studies reviewed in this paragraph have been conducted with student samples and research on the action perception-production coupling in middle-aged adults (i.e., 40 to 60 years) is lacking. Therefore, it is not clear whether the reported variations are also influenced by participants' age.

2.3 Interrelation of action perception and production in older adults

To date, there is only a small amount of studies looking at the action perception-production coupling in late adulthood. The findings of these studies suggest that the mechanisms involved in the processing of actions change as people get older (Saimpont, Malouin, Tousignant, & Jackson, 2013; Saimpont, Mourey, Manckoundia, Pfitzenmeyer, & Pozzo, 2010; Skoura, Papaxanthis, Vinter, & Pozzo, 2005). For instance, Gabbard, Caçola, and Cordova (2011) asked adults and older adults to indicate whether an object is within reaching distance or out of reach. Adults over the age of 65 years were less precise in their judgments than younger adults and reported the objects to be within reaching distance, even if they were not. In another series of studies, older participants showed a decreased ability to predict the time-course of a partly occluded movement (Diersch et al., 2013, 2012).

Additionally, in this and other studies, older adults recruited a wider network of cortical areas during action observation, showed less selective modulation of corticospinal excitability and especially activated visual brain areas to a greater extent than did young participants (Diersch et al., 2013; Léonard & Tremblay, 2008; Nedelko et al., 2010). This heightened reliance on visual information processing during action perception has been found in other studies as well (Costello & Bloesch, 2017).

Taken together, the studies reviewed in the preceding sections indicate differences in action perception and action production between age groups. During childhood, action perception and production are tightly coupled and increase in quality. In adulthood, perception and production elicit reciprocal influences on each other, are altered in response to experience and change with advancing age. In the next chapter, possible reasons for these differences are discussed. Furthermore, it is highlighted how the interrelation of action perception and production may develop across the life span.

3. Explaining life-span differences

What is it about age that results in the age-related differences in action perception and production? Advancing age in infancy and childhood goes along with the development of social and emotional skills (Bukowski, Laursen, & Rubin, 2009) as well as an increase in motor (Gallahue et al., 2012; Payne & Isaacs, 2008) and cognitive abilities (Kochanska, Coy, & Murray, 2001). For example, children get increasingly proficient in locomotion, develop their fine-motor skills (Adolph & Berger, 2006), and show better performance in executive function tasks (Zelazo, Müller, Frye, & Marcowitch, 2003). In late adulthood, increasing age is accompanied by a decrease in cognitive functioning (e.g., working memory capacity or executive functions; Salthouse, 2005, 2009), poorer health (Leist, Kulmala, & Nyqvist, 2014), changes in social networks (Holmén & Furukawa, 2002) and differences in emotion regulation (Brassen, Gamer, Peters, Gluth, & Buchel, 2012) as well as a decline in motor abilities (Houx & Jolles, 1993; Kauranen & Vanharanta, 1996). For instance, older adults show heightened risk of falls (Sattin, 1992) and a decreased inhibition of automatized reactions (Korsch, Frühholz, & Herrmann, 2014).

All of these factors might contribute differently to life-span variations in action perception, production, and their interrelation. Therefore, a theoretical framework is needed to integrate different age-related influences. While most approaches, which aim to explain developmental processes – such as the interactive specialization approach (Johnson, 2000, 2001) or the Scaffolding Theory of Aging and Cognition (STAC; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) – have been concerned with narrow age ranges, their main assumptions may be summarised within one life-span perspective (Baltes, 1987; Baltes, Reese, & Lipsitt, 1980). According to this view, development is to be seen as life-long process of growth and loss. Against the common presumption that abilities increase in quality and quantity during childhood and experience a decrease towards late adulthood, this perspective assumes them to improve, drop or vanish at any age. Development in one domain (e.g., motor) is assumed to influence the development in another domain (e.g., cognition). Also, intra-individual change is hypothesised to depend on the context and specific experiences the individual makes in such that development is the result of an interaction between the individual and the (culturally and historically) changing environment (Baltes, 1987; Baltes et al., 1980). All of these assumptions find an equivalent in an explicit theoretical framework, the *complex dynamic system approach* (Thelen & Smith, 1994). This approach allows explaining and predicting age-related changes across the life span.

3.1 A theoretical approach

Within the complex dynamic systems approach (Thelen & Smith, 1994; van Geert & Steenbeek, 2005), life-span development is understood as a self-organising process. Observable behaviour is assumed to result from the real-time interaction of various components (Smith & Thelen, 2003). The coordination of these components is nonlinear, context-dependent, and takes place on several hierarchic levels. An example for such a dynamically coordinated and hierarchic system is the brain, which is comprised of different interacting cortical areas, which themselves are made out of multiple layers of tissue, which again accommodate numerous neurons (Thelen & Smith, 1994).

The observed behavioural output of a complex dynamic system is highly adaptive to the individual's internal and external constrains (Thelen & Smith, 1994; van Geert, 2011; van Geert & Steenbeek, 2005). For instance, infants, at birth, spontaneously perform stepping movements when held upright. However, this behaviour disappears at around 2 months of age (Thelen & Smith, 1994). According to the complex dynamic system approach, such observable changes in behaviour across development occur when one or more major components (*control parameters*) of the system change beyond a certain threshold (Thelen & Smith, 1994; van Geert & Steenbeek, 2005). As a result, the system is destabilised, the associations between the components are disorganised and the complex dynamic system gradually shifts from this unstable to a new stable state (*phase transition*). In the case of stepping, it has been shown that infants gain weight rapidly in the form of fat in the first months of their lives. This puts load on the less developed muscles and stepping in the upright position becomes increasingly more demanding and less adaptive (Thelen & Smith, 1994).

Hence, within the complex dynamic system approach, development is not seen as a steady increase of stability during childhood and a respective decrease in late adulthood, but as a series of continuously changing states of relative stability and instability of the system. Nevertheless, phase transitions are assumed to be more frequent at the beginning and towards the end of the life span (Thelen & Smith, 1994). This is in line with other theoretical approaches to development (Johnson, 2000; Park & Reuter-Lorenz, 2009), which assume a flexible cortical organisation across development. They as well predict increasingly narrower cortical response patterns with increasing age during childhood and an again broadening towards late adulthood.

In line with the principles of the complex dynamic system approach, the age-related and observable differences in action perception and production may be seen as the developmental output of the interaction between various components. These components may include factors within the domains of cognitive, emotional, social and motor development mentioned at the beginning. Together, these components spontaneously organize themselves into a self-sustained state (*attractor state*). That is, cognitive, emotional, social, and motor components find a stable pattern in their individual characteristics and interactions with each other across hierarchy levels (Thelen & Smith, 1994; van Geert, 2011). This state is robust against perturbations and the system goes back to it when pushed out of it. On the behavioural level, the relative rigidity or flexibility of such a state can be approximated by measuring recurrence in participants' behaviour (or gaze behaviour as discussed in chapter 1.1; Anderson et al., 2013). Reduced recurrence is an indicator of relative instability of the complex dynamic system. Two factors are assumed to have a particularly strong impact on the dynamics of the complex system, resulting in observable action perception and production. These two control parameters are the participants' action experience and their motor competence.

Action experience describes the size of individuals' motor repertoire. It represents our accumulated active experience with producing and processing different kinds of actions (Kontra, Goldin-Meadow, & Beilock, 2012). In contrast, *motor competence* is defined as the individuals' maximal performance level or their potential in the quality and speed of movement execution and summarises participants' gross and fine motor skills (Haywood & Getchell, 2005). Both of these parameters are related to the sensorimotor system (e.g., Catmur et al., 2008; Karni et al., 1998) and therefore likely to alter how we perceive and produce actions (for an overview see Hunnius & Bekkering, 2014). While surely overlapping in origin, these two factors are distinct in their developmental trajectories and their influences on the action perception-production coupling. Therefore, the next paragraph focuses on more detailed definitions of action experience and motor competence as well as a description of their relations to action perception and production as shown by previous studies.

3.2 Action experience and motor competence

Action experience results from learning (Schmidt & Lee, 1999). It refers to the accumulated life-long gain in sensorimotor experiences with the production of actions (Kontra et al., 2012). That is, as we get older, it is very likely that we engage in different kinds of actions in our interaction with others and our environment. This leads to a broadening of our motor repertoire across the life span (Kontra et al., 2012; Loeffler, Raab, Cañal-Bruland, & Rodger, 2016).

In infants, action experience changes how they perceive actions (Cook, Bird, Catmur, Press, & Heyes, 2014; Daum et al., 2011; Sommerville & Woodward, 2005; Stapel, Hunnius, Meyer, & Bekkering, 2016; Verschoor, Spapé, Biro, & Hommel, 2013) and alters the activity of their sensorimotor system during action perception and production (Meyer, Braukmann, Stapel, & Hunnius, 2016; Paulus, Hunnius, Van Elk, & Bekkering, 2012; Virji-Babul, Rose, Moiseeva, & Makan, 2012). For instance, after giving 3-month-olds the opportunity to make a grasping experience using sticky Velcro-covered mittens, they were more likely to perceive a grasping action as goal-directed than without this experience (Sommerville, Woodward, & Needham, 2005). This effect was unique to active action experience (Gerson & Woodward, 2014). Action observation experience alone was not associated with a similar facilitation of action-goal perception (Gerson & Woodward, 2014) and the related changes in the activation pattern of the sensorimotor system in this study (Gerson, Bekkering, & Hunnius, 2015).

Action experience also influences the perception of actions in adults. For instance, participants were more accurate in predicting action goals in video-recordings of their own actions than in recordings of other people (Knoblich & Flach, 2001; Knoblich et al., 2002).

Also on the neural level, the activity of sensorimotor brain regions during action perception varies with the observers' previous action experience (Catmur et al., 2008; Catmur, Walsh, & Heyes, 2009; Heyes, 2010; Press, Heyes, & Kilner, 2011).

Motor competence refers to fundamental motor skills. These include locomotor skills (the ability to move one's body through space) as well as object control skills (the ability to manipulate objects; Haywood & Getchell, 2005; Payne & Isaacs, 2008). They can further be categorised into gross and fine motor skills. While gross motor skills involve the movement of larger muscle parts (e.g., movement of legs while walking), fine motor skills describe more fine-tuned movements (e.g., movement of fingers in grasping a pen; Gallahue et al., 2012; Santrock, 1999).

Motor competence increases across childhood (Adolph & Berger, 2011; D'Souza, Cowie, Karmiloff-Smith, & Bremner, 2017), peaks between 19 to 26 years of age (Santrock, 1999), and decreases again in later adulthood (Houx & Jolles, 1993; Kauranen & Vanharanta, 1996) as a result of maturational (Thelen & Smith, 1994) and dedifferentiation processes (Heuninckx et al., 2005; Heuninckx, Wenderoth, & Swinnen, 2008) as well as a dynamic interaction of the individual with its environment (Thelen & Smith, 1994; von Hofsten, 2004). During their first years of life, children gain prospective control over their actions (von Hofsten & Rönnqvist, 1988) and increasingly master goal-directed movements (D'Souza et al., 2017; von Hofsten, 2004). Late adulthood is accompanied by less precise motor planning (Reuter, Behrens, & Zschorlich, 2015), and an increase of activation in the sensorimotor system (Heuninckx et al., 2005; Ward & Frackowiak, 2003; Ward, 2006). In general, motor competence is associated with the cortical representation of sensorimotor information (Bowman et al., 2017; Karni et al., 1998; Matsuzaka, Picard, & Strick, 2007; Poldrack et al., 2005) and increased levels are related to a more automated information processing (Rémy, Wenderoth, Lipkens, & Swinnen, 2010; Wu, Kansaku, & Hallett, 2004). Therefore, higher levels of motor competence should be associated with higher levels of action perception and production.

In line with this, motor competence for specific actions is associated with increased performance in action perception tasks. Motor experts (e.g., professional athletes or musicians) have higher abilities or higher maximal levels in performing their action of expertise as a result of intensive training. They predict the correctness of a partially occluded movement continuation more accurately than novices (figure skating: Diersch, Cross, Stadler, Schütz-Bosbach, & Rieger, 2012; tennis: Farrow & Abernethy, 2003). Furthermore, their gaze behaviour differs from non-experts when perceiving their action of expertise (e.g., areas of fixations, number of saccades; Gegenfurtner, Lehtinen, & Säljö, 2011). For example, goalkeepers showed less fixations but higher fixation durations when observing penalty kicks compared to novices (Savelsbergh, Williams, Van Der Kamp, & Ward, 2002). On the neural level, motor experts show greater sensorimotor activation during the perception of “expert” actions than for actions for which they only possess visual experience (e.g. dancers: Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006; Cross, Hamilton, & Grafton, 2006; volleyball, badminton and tennis players: Balser et al., 2014; Wright, Bishop, Jackson, & Abernethy, 2011; pianists: Haslinger et al., 2005; Haueisen & Knösche, 2001). To sum up, these studies show that specific motor competence is associated with higher levels of action perception and production of the “expert” action. However, to date, research was concerned with motor competence for very specific actions only and no study has looked at the influence of motor competence across actions.

Taken together, the studies reviewed so far indicate that action experience and motor competence both influence action perception and production. The two factors surely overlap because they both develop as a result of the individual’s interaction with its environment. The more actions we produce, the broader our action experience becomes and the greater the likelihood that we train our fundamental motor skills and increase our level of motor competence. However, action experience and motor competence are also distinct. Action experience refers to the size of our motor repertoire, motor competence describes our maximal performance level in movement execution. The two factors also follow different life-long trajectories. While action experience increases with age, motor competence shows an inverted U-shaped trajectory.

Hence, to conclude the preceding sections, the complex dynamic system approach may be seen as a promising candidate for describing and explaining how action perception and production are coupled across the life span and related to action experience and motor competence. From a life-span perspective, the approach predicts more frequent phases of destabilisation and reorganisation within the dynamic system in childhood and towards late adulthood compared to more stable phases during adulthood (Johnson, 2000; Park & Reuter-Lorenz, 2009; Thelen & Smith, 1994). Consequently, this thesis has two levels of theorizing. While details of the action perception-production coupling are embedded within more narrow theories (e.g., common-coding approach, simulation theory) introduced at the beginning, the complex dynamic system approach opens up a life span perspective and will be used to describe dynamic differences in the coupling that are related to action experience, motor competence, or age.

4. Empirical studies

The main question that guided the research of the current thesis was to describe the action perception-production coupling across the life span by employing comparable research designs and methodologies. The particular approach to this general question, the derived sub questions, and the methods applied are described in the next sections. I will start with a discussion of the limitations of previous work. From these shortcomings, the research question of the current thesis is derived and steps, which have to be undertaken to answer this question, are summarised. Finally, the specific research questions, hypotheses, designs, and main findings of the three studies constituting this thesis are reported.

4.1 Research gap

As discussed above, previous research indicates that action perception and production are interrelated from early on and change across the life span. Furthermore, the individuals' previous action experience and their motor competence also contribute to these age-related inter-individual differences. Therefore, the interrelations of action perception and production can be expected to experience quite an amount of variability across individuals (of different ages). However, our knowledge on the action perception-production coupling is so far based on studies investigating selective age groups. Furthermore, some age groups (e.g., children, adolescents, middle-aged adults) have been neglected almost completely in previous work. Also, different measurement techniques (e.g., eye tracking, EEG, fMRI) and dependent variables (e.g., action anticipation, desynchronisation of the mu-rhythm) were employed. These issues make it difficult to compare findings across studies and age groups. Therefore, no coherent picture of the interrelations of action perception and action production across the life span is possible to this date. That is, it is not known whether action perception and production follow the same life-span trajectory or whether their coupling is influenced by age-related influences as well.

4.2 Research question

The current project aims to set the first cornerstone in filling this gap in research by describing the action perception-production coupling across the life span and by employing comparable research designs and methodologies. To achieve this aim, (a) action perception and production were investigated across the whole life span and participants between the ages of 3 and 80 years were recruited. Furthermore, (b) comparable research designs and measures were used for all participants. That is, action perception was measured via eye tracking. This technology does not require special preconditions and it is therefore applicable to children and adults (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003). The last step was then to (c) provide a coherent picture of the life-long differences in the interrelations of action perception and production. For this, the individual life-span trajectories of action perception and action production were established first. Second, their bi-directional influences on each other on an immediate and a deferred level were addressed. Third, the associations of action experience and motor competence with the action perception-production coupling were explored. In line with this, the following three major questions guided the research:

1. How do action perception, action production and their interrelations differ across the life span – from childhood to late adulthood? (*Study I*)
2. How does the influence of action perception on simultaneous action production differ across the adult life span? (*Study II*)
3. How does the influence of action production on simultaneous action perception differ across the adult life span? (*Study III*)

Furthermore, in these three studies, development was understood as a self-organising process and differences in the observable behaviour were seen as the output of a complex dynamic system. Within this system, two major control parameters – the individuals' action experience and their motor competence – were assumed. These two parameters were expected to interact in a nonlinear and context-dependent manner. Therefore, task-specific relative contributions of these two parameters were hypothesised. In the next section, the research questions, hypothesis, methods, and main findings of the studies constituting this dissertation are summarised.

4.3 Study summaries

The following study summaries build the basis for the subsequent discussion. For a more detailed description of the methods employed and results obtained please see the original studies in Part II of this thesis. Please note that the three studies are part of a larger longitudinal research project on the interrelations of action perception and production throughout childhood and adulthood. The tasks employed in this project were designed to assess participants' oculomotor skills (e.g. smooth pursuit, saccade velocity) along with their action perception and their accuracy and speed in action production. Furthermore, several additional measures such as the participants' health status, handedness, and motor or cognitive skills were included. Hence, the participant samples of the three studies summarised below are overlapping cross-sectional subsamples of all participants tested in the longitudinal project.

Study I: How do action perception, action production and their interrelations differ across the life span – from childhood to late adulthood?

This study explored the developmental trajectories of action perception and action production and investigated how action production influences action perception across the life span. Action production was assumed to follow an inverted U-shaped trajectory across the life span because of its strong correlation with motor competence. That is, the ability to perform a certain action is strongly influenced by the individual's general motor skills (Gallahue et al., 2012). Action perception was expected to either increase linearly with age or follow an inverted U-shaped trajectory. That is, on the one hand, action perception was assumed to be affected by the individuals' accumulated action experience (e.g., Gerson & Woodward, 2014; Knoblich & Flach, 2001) and therefore to parallel its life-long increase (Kontra et al., 2012). On the other hand, the participants' motor competence was also expected to influence action perception (e.g., Calvo-Merino et al., 2006) resulting in a more curvilinear trajectory (Adolph & Berger, 2006; Houx & Jolles, 1993). Finally, the deferred influence of action perception on action production was assumed to be moderated by the participants' age (Diersch et al., 2012; Gampe et al., 2015).

Participants ($N = 214$; 3-80 years) were asked to observe either a familiar or an unfamiliar multistep action and to subsequently reproduce the according action (task adapted from Gampe, Prinz, & Daum, 2015). Action perception was measured via the participants' anticipation of action goals (anticipation frequency) and recurrence quantification analysis of participants' fixation sequence. The recurrence rate was used as an indicator of the stability of participants' gaze behaviour. Action production was assessed via the accuracy of participants' reproduction of the observed actions.

For the familiar action, participants' age was not associated with their action perception (as indicated by anticipation frequency and recurrence rate). For the unfamiliar action, participants' anticipation frequency increased with advancing age and their recurrence rate was reduced in childhood and towards late adulthood compared to the middle of the life span. The accuracy of action production followed an inverted U-shaped life-long trajectory for both actions. Finally, participants' action production ability of unfamiliar action was negatively associated with the recurrence rate in their gaze pattern across the life span.

Taken together, these results support the assumption that participants' action experience influences their action perception as measured via anticipation frequency. However, when measured via recurrence, participants' action perception showed to be less stable at the beginning and the end of the age span measured. Similarly, the life-long trajectory of action production paralleled the development of motor competence across the life span. Finally, the findings suggest that the deferred influence of action perception on action production remains stable across age groups. In sum, the observed age-related differences in action perception and production may be seen as a dynamically changing system, which does not follow linear pathways.

Study II: How does the influence of action perception on simultaneous action production differ across the adult life span?

The second study investigated how advancing age during adulthood affects the magnitude of interference in action production during simultaneous and incongruent action perception. Based on previous findings, incongruent action perception and production were assumed to interfere with each other if they were performed simultaneously (Brass et al., 2000; Brass, Zysset, et al., 2001). Furthermore, since previous work reports less specialised information processing in the sensorimotor system with advancing age (and reduced motor competence) in adulthood (Léonard & Tremblay, 2008; Mouthon, Ruffieux, Keller, & Taube, 2016), this interference effect was expected to increase with age.

In a task adapted from Brass et al. (2000), participants (N = 157; aged 20-80 years) were asked to respond to a visually presented finger movement (*movement condition*) and/or symbolic cue (*symbolic condition*) by executing a previously defined finger movement. In *baseline trials*, only the finger movement or only the symbolic cue was shown. In *congruent trials*, finger movement and symbolic cue appeared at the same time and indicated the same response finger. In *incongruent trials*, the simultaneously presented movement and cue indicated contradictory response fingers. Action production was assessed via participants' reaction times (RTs).

Participants' RTs were longer in incongruent compared to congruent and baseline trials. More detailed analyses on the incongruent trials show that participants were slower in trials in which they were asked to ignore an incongruent finger movement (*motor interference*) compared to trials in which they had to ignore an incongruent symbolic cue (*symbolic interference*). Moreover, advancing age was shown to accentuate this effect. That is, the difference in the two interferences got greater as the participants' age increased. These findings indicate that the simultaneous processing of perceived and produced actions results in an interference effect that goes beyond the effect of having to process two conflicting stimuli at the same time. Furthermore and in line with the assumption of a less precise internal processing of actions within the sensorimotor system with advancing age, the motor interference effect was accentuated in older participants.

Study III: How does the influence of action production on simultaneous action perception differ across the adult life span?

In this study, it was investigated whether age-related differences in fine-motor competence affect the interference effect of action production on simultaneous action perception. Previous research indicates that lower levels of motor competence are associated with less automated information processing (Rémy, Wenderoth, Lipkens, & Swinnen, 2010; Wu, Kansaku, & Hallett, 2004) and with a higher assumed vulnerability of the sensorimotor system to challenges (such as the simultaneous processing of action perception and production). Therefore, age-related decreases in fine-motor competence were assumed to be associated with increased interference, while higher levels of fine-motor competence were assumed to be associated with lower interference effects in simultaneous action perception and production.

In a cross-sectional eye-tracking study, adult participants ($N = 181$, 20-80 years) observed a manual grasp-and-transport action while performing an additional motor or cognitive distractor task (adapted from Cannon & Woodward, 2008). Action perception was measured via anticipation frequencies. Fine-motor competence was assessed with the Motor Performance Series (Neuwirth & Benesch, 2011). The interference effect in action perception was greater in the motor than in the cognitive distractor condition. That is, participants anticipated fewer action steps if they were asked to simultaneously perform a different action (*motor distractor task*) than if they were asked to mentally rehearse a set of digits and letters (*cognitive distractor task*). Furthermore, fine-motor competence and age in years were both associated with this interference. The better the participants' fine-motor competence and the younger they were, the smaller the interference effect. However, when both influencing factors (age and fine-motor competence) were taken into account, a model including only age-related differences in fine-motor competence was shown to better account for the data at hand. In line with the results of *Study II*, the current findings point to an increase in interference in simultaneous action perception and production with advancing age. They furthermore suggest that motor competence affects the action perception-production coupling across the adult life span.

5. Discussion

This thesis aimed at describing the action perception-production coupling across the life span by employing comparable research designs and measures. The findings of the three studies constituting this thesis indicate an increase of action perception and action production during childhood and a relatively stable level in adulthood (*Study I*). In late adulthood however, action perception was shown to increase in terms of anticipation frequency (*Study I* and *Study III*) and to decrease when looking at the recurrence rate in participants' gaze behaviour (*Study I*). Action production decreased with advancing age in adulthood (accuracy: *Study I*; speed: *Study II*). The findings on the action perception-production coupling indicate a relatively stable deferred influence of perception on production across the life span (*Study I*). In contrast, the immediate influences within the coupling were accentuated towards late adulthood (*Study II* and *Study III*).

5.1 Evaluation of operationalization

To answer the overall research question of this thesis, several interim steps were proposed in the process. The first step was to (a) investigate action perception and production in participants across the entire life span. In *Study I*, individuals between the ages of 3 and 80 years participated. *Study II* and *Study III* focused on adults between 20 and 80 years. This reduction to the adult life span in two of the studies allowed controlling for factors that might have influenced participants' performance (e.g., cognitive skills, attention or health status). Nevertheless, the current findings cover a large part of the life span, which distinguishes them from previous studies.

The second step was to (b) use comparable measures and research designs. In all studies of this thesis, eye-tracking technology was used to measure action perception. This technology is especially useful for life span overarching studies because it allows measuring performance without the need of giving participants detailed instructions. Furthermore, it is non-invasive and to a certain degree robust to movements of the participants (Gredebäck et al., 2010). Action production was measured via the accuracy of participants' imitation of simple actions (*Study I*) or the speed of action initiation and execution (*Study II*). Imitation tasks are widely used in work on children, adults, and older adults (Gampe et al., 2015; Léonard & Tremblay, 2008). However, advancing age in late adulthood is related to a general slowing (Salthouse, 1996) and reduced speed in dual-tasks in particular (Korsch et al., 2014; Maquestiaux, 2016), which might have biased RT measures. These issues were accounted for by baseline-correcting the target RTs and comparing them to RTs in an action-unrelated dual-task. Hence, it is sensible to conclude that the measures used were applicable to the participants investigated and the initial requisite of comparable measures was met. Judging the comparability of the applied research designs is less straightforward. Especially the participants' anticipatory eye movements are shown to be influenced by age (Pratt, Dodd, & Welsh, 2006; Rosander & von Hofsten, 2011), gender (Kenward et al., 2017), or speed and type of action (Daum, Gampe, Wronski, & Attig, 2016; Gredebäck, Stasiewicz, Falck-Ytter, von Hofsten, & Rosander, 2009). Therefore, the participants' anticipation frequencies were compared to task-specific baselines (*Study II* and *Study III*) and to the recurrence in their fixation sequence as a second measure of action perception (*Study I*). Furthermore, other (age-related) factors such as the participants' cognitive skills, health, attention, or situational and motivational aspects might have influenced their performance in the tasks in general. Some of these factors have been measured and controlled for (*Study II* and *Study III*). Additionally, the current findings replicated previous single age groups studies (Brass et al., 2000; Cannon &

Woodward, 2008; Gampe et al., 2015) across larger age ranges, pointing to rather comparable research designs across age groups.

The last step was to (c) provide a coherent picture of the life-long differences in the interrelations of action perception and production. This step was achieved by reporting the life-long trajectories of action perception and action production. Moreover, the coupling of the two of them was investigated in both directions, from perception on production and vice versa. The contributions of action experience and motor competence were explored by measuring motor competence in adults with a standardized battery (Neuwirth & Benesch, 2011) and approximating action experience with participants' age. To conclude, while the findings do have their limitations (discussed below), the overall aim of describing the life-long trajectories of the action perception-production coupling was met.

The three studies fulfilled the interim steps that were proposed in answering the research question. On this basis, the findings of the studies can be discussed and integrated on the theoretical and empirical level.

5.2 Theoretical and empirical integration of findings

Within this paragraph, the central findings of the three studies of this thesis are reconsidered with regard to the literature reviewed in the introduction. There, three major assumptions were derived from theoretical frameworks on the action perception-production coupling. The current thesis provides empirical support for these assumptions. The first of these core assumptions was that (1) action perception and production are processed in overlapping resources within the sensorimotor system. While no study of this thesis measured sensorimotor activity directly, one may infer overlapping processing resources form the findings on the immediate effects of action perception on production and vice versa (*Study II* and *Study III*). Since the sensorimotor system is already tuned in for a certain action when perceiving it, the concurrent production of an incongruent action interferes with this movement preparation (Blakemore & Frith, 2005). Also the common-coding approach

(Hommel et al., 2001) predicts that, in cases in which perception and production simultaneously tap into the same codes, they may interfere with each other. The findings of *Study II* and *Study III* show such interference effects in both directions. Furthermore, they also point to age-related differences in the processing overlap. However, neural measures would be needed to further support this assumption. From these measures we would gain insights into which cortical areas are involved in the immediate effects of the action perception-production coupling and how age affects these areas. That is, according to the dedifferentiation hypothesis (Li & Lindenberger, 1999), advancing age is associated with less specialized processing and recruitment of brain areas. In line with this, it has been shown that perceptual and motor information is represented less distinctly with advancing age (Carp, Park, Hebrank, Park, & Polk, 2011; Carp, Park, Polk, & Park, 2011), which might be one contributor the observed accentuation of interference effects towards late adulthood (*Study II* and *Study III*).

The second core assumption of the reviewed theoretical frameworks was that (2) actions are processed in an anticipatory manner. In line with this, the findings of *Study I* support prior work showing that the anticipation of action goals is already present in young children (Gampe et al., 2015; Gredebäck et al., 2009). The same results also point to an increase in anticipation frequency during adulthood. This contrasts previous findings with older adults, which report age-related decreases in the ability to predict the time-course of a partially occluded action (Diersch et al., 2013, 2012). However, in these studies, the participants' task was to internally preserve the exact temporal structure of the action, which calls for precise processing and simulation of actions (Stadler et al., 2011). In *Study I* and *Study III*, participants were asked to observe simple action sequences, while their anticipation of the according action steps was measured. Therefore, the obtained anticipation frequencies might be less influenced by the precision of internal action simulation and rely more on the individuals' action experience (as discussed in the next paragraphs). Finally and in line with previous research (Cannon & Woodward, 2008), *Study III* indicates that the anticipation of actions is influenced by the concurrent production of an action.

The third core assumption of the reviewed framework proposed (3) changes in the action-production coupling, for instance in response to acquiring experience with actions. While conclusions about change cannot be drawn if change is not what is being measured, the current findings nevertheless indicate that participants differ in action perception, production and the coupling between the two of them depending on their age, action experience, and motor competence. The nature of these differences was proposed to be the result of a dynamic, non-linear, and self-organised process (Thelen & Smith, 1994; van Geert & Steenbeek, 2005). The current findings provide support for this proposition of a complex dynamic system underlying the interrelations of action perception and production in several ways.

First, children and older adults showed reduced recurrence in their gaze behaviour compared to younger and middle-aged adults (*Study I*). This is in line with the presumption of the complex dynamic systems approach of more frequent phase transitions in childhood and late adulthood (Thelen & Smith, 1994). Less recurrent behaviour indicates less stable states and reorganizational processes within the complex dynamic system. The results of *Study I* therefore point to the predicted inverted U-shaped trajectory of the complex dynamic system's stability across the life span. Second, the reported life-long trajectories of action perception, action production and their coupling support the assumption of action experience and motor competence being control parameters within the complex dynamic system. That is, action experience and motor competence were assumed to initiate shifts in observable behaviour when changing beyond a critical threshold (Thelen & Smith, 1994). Their strong influence on the dynamics of the system was assumed because of their common basis with action perception and production within the sensorimotor system (Bowman et al., 2017; Karni et al., 1998; Matsuzaka et al., 2007).

Action experience and motor competence follow a parallel developmental direction towards higher levels across childhood (Adolph & Berger, 2006; Gallahue et al., 2012; Payne & Isaacs, 2008). Hence, the combination of their relative contributions predicts the observed linear increase in action perception and production as well as the stable coupling between the two of them in young participants (as observed in *Study I*). In adulthood, action experience continues to increase (Kontra et al., 2012), while motor competence first remains relatively stable and then decreases in older adults (Payne & Isaacs, 2008; Santrock, 1999). Therefore, predictions of the behavioural outcomes in action perception and action production are less straightforward and their trajectories are shown to vary across the adult life span. In particular, action perception increased in adult years, paralleling the continuous accumulation of sensorimotor experiences with different actions (Kontra et al., 2012; Loeffler et al., 2016; Pilz, Bennett, & Sekuler, 2010). Action production decreased towards late adulthood in line with the previously reported age-related decrease in motor competence (Heuninckx et al., 2005; Reuter et al., 2015; Ward, 2006; Ward & Frackowiak, 2003). Furthermore, the relatively stable deferred influence of action perception on production across adulthood may be seen as an observable lead on the buffering effect of life-long accumulated action experience. That is, while advancing age in late adulthood and the associated dedifferentiation processes are shown to weaken the functionality of the sensorimotor system (Heuninckx et al., 2005; Sharma & Baron, 2014; Ward, 2006; Ward & Frackowiak, 2003), increased action experience might make it more robust to stressors (Capa et al., 2011; Diersch et al., 2012, 2016; Roberts et al., 2016). In contrast, the immediate influences within the action perception-production coupling point to a strong influence of motor competence and the flexibility of the sensorimotor system that comes with it (Poldrack et al., 2005). Specifically, in the current studies, older adults were affected more by the perturbations of the simultaneous processing of perceived and produced actions than younger adults (*Study II* and *Study III*). Increased levels of motor competence weakened this age-related effect (*Study III*). In line with these findings, increasing age is associated with less flexible processing of actions (Boisgontier & Nougier, 2013; Moran, Symmonds, Dolan, & Friston, 2014). Contrariwise, higher levels of motor competence are shown to result in more automated sensorimotor processing (Rémy et al., 2010; Wu et al., 2004). This frees resources and allows for higher processing flexibility in challenging situations (such as simultaneous action perception and production).

Taken together, the findings of this thesis point to a complex dynamic system in which action perception and production are closely intertwined with each other across the entire life span. Action experience and motor competence affect this intertwining and help stabilize the system’s attractor state. Furthermore, depending on the individual’s age and the task at hand, they interdigitate with the coupling more or less strongly and this result in different observable behaviours.

5.3 Limitations and future directions

The current thesis aimed at describing the interrelations of action perception and production across the life span. The preceding discussion has highlighted the influences of action experience and motor competence on the trajectories found. However, other factors may also alter the action perception-production coupling. For instance, previous research indicates that individuals of different age groups weight incoming information differently (Costello & Bloesch, 2017). That is, children are shown to rely strongly on motor information while older adults focus more on visual information when perceiving and producing actions (Diersch et al., 2013; Frick, Daum, Wilson, & Wilkening, 2009). This emphasis of visual over motor information is adaptive for older individuals since advancing age is associated with less distinct sensory input and dedifferentiation processes within the sensorimotor system (Bernard & Seidler, 2012; Heuninckx, Wenderoth, & Swinnen, 2010; Koppelmans, Hirsiger, Mérillat, & Seidler, 2015). Nevertheless, the shift in focus might influence the dynamics within the complex system and result in a decoupling of action perception and production in later adulthood (Costello et al., 2014; Costello & Bloesch, 2017). In line with this, older adults also recruit hippocampal areas during action perception, indicating more top-down influences of memory processes (Diersch et al., 2013). Another drawback of the current studies is their cross-sectional design. Specifically, the findings of this thesis propose intra-individual differences in action perception and production based on the observer's/ agent's age, motor competence, and action experience. However, the life-long developmental change in these interrelations and the inter-individual differences in their change have yet to be investigated using longitudinal designs.

Additionally, action experience has been approximated with the participants' age for this thesis. Therefore, the relative contributions of age and action experience on the obtained result patterns are still unknown. To disentangle the unique effects of age and action experience, an assessment tool to measure the life-long accumulated experience with different actions is needed. Alternatively, one may experimentally induce sensorimotor experience with a specific (unfamiliar) action in participants of different age groups through training (Figure 1 for more detailed design).

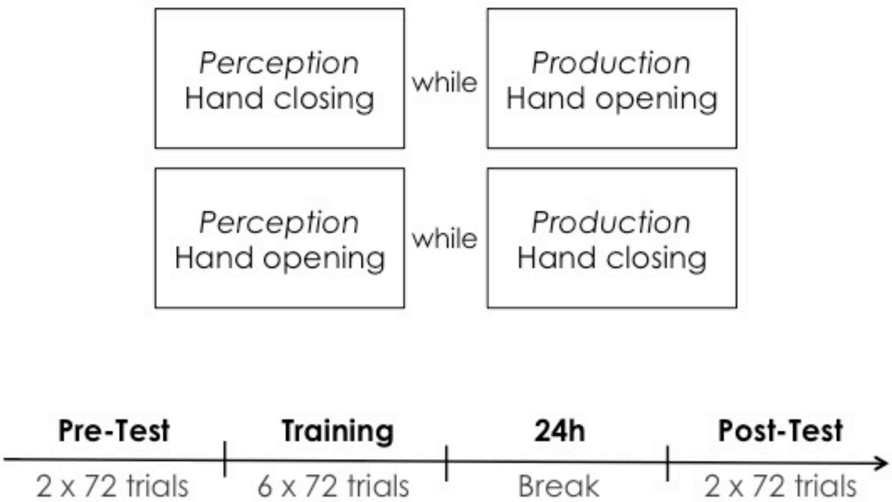

Figure 1. Research design of follow-up project (adapted from Heyes et al., 2005). Participants of different age groups (children, adults, older adults) are trained with an unfamiliar action. Prior and after this training, the participants' RTs in reacting to these stimuli is measured.

Within this study, participants would receive sensorimotor training in opening their hand while observing a hand closing action or vice versa (task adapted from Heyes et al., 2005). In line with the original study, interference effects in simultaneous action perception and production should be reduced after training. This design not only allows assessing the influence of action experience on the action perception-production coupling independent of age group, but also the measurement of learning rates. The analysis of the participants' progress in acquiring a new action, and the processes involved in this learning, would give new insights into the dynamics in the action perception-production coupling. Furthermore, when recruiting participants with varying degrees of motor competence, one would be able to analyse the contribution of the participants' initial motor competence on the learning process. Specifically, one would expect participants with higher levels of motor competence – independent of age group – to profit more from sensorimotor training with an action (Hund-Georgiadis & von Cramon, 1999; Voelcker-Rehage & Willimczik, 2006; Yang, 2015).

5.4 Conclusion: What do we learn from the three studies?

The findings of this thesis have implications on the methodical, applied and theoretical level. On the methodical level, the current project bridges the still existing gap between research on children and research on adults. On a great part this gap is due to the incompatibility of research methods applied and the lack of life span overarching theoretical frameworks. For this thesis, an assessment method (eye-tracking technology) and a theoretical framework (complex dynamic system theory) were applied, which were suitable for children, adults and older adults. This resulted in comparable findings on the action perception-production coupling across the entire life span. Most importantly, these or similar practices may be applied to other fields of research as well, clearing the way for research on the whole life span (Smith & Thelen, 2003; van Geert, 2011; van Geert & Steenbeek, 2005).

On the applied level, the findings of the three studies add to the empirical basis for clinical applications. That is, the notion of shared processing resources for action perception and production has been used in stroke or brain injury rehabilitation – especially in older patients (Tia et al., 2010). Evaluations of such training protocols indicate that when motor training in producing certain actions is accompanied by action perception and motor imagery, this helps regaining motor skills (Wulf, Shea, & Lewthwaite, 2010) and results in increased force production (Porro, Facchin, Fusi, Dri, & Fadiga, 2007). However, empirically the training protocols are built on research with young adults. With the current findings a more accurate picture of action perception, production and their interrelation in healthy children, adults and older adults is provided. For instance, the current findings suggest that older patients profit more if they possess higher levels of motor competence. Hence, the findings of this thesis might foster more adaptive training protocols and respective gains in rehabilitation.

On the theoretical level, this thesis began by stating that the ability to understand others' actions is a cornerstone of human culture (Rizzolatti & Craighero, 2004), which is based on the interrelation of action perception and production (Hommel et al., 2001; Prinz, 1990). The studies constituting this thesis were the first to describe the life-span trajectories of these interrelations. Taken together, the findings illustrate that a toddler, his father, or his grandmother are very likely to perceive actions differently. While we are able to understand other people's actions as being directed towards goals from early on (Woodward, 1998), this understanding is based on our constantly changing ability to act within and on the world. Consequently, social interaction, cooperation, joint action, and social learning are affected by the individual characteristics of the interaction partners – their age, action experience and motor competence. This issue might explain why communication and our coexistence sometimes fail and it gives rise to research on the exact mechanisms involved in these processes.

Finally, coming back to the initial example, what do the current findings say about the chances of the keynote speaker to catch his train? The studies predict different probabilities of success, depending on the speaker's age as well as his previous and current lifestyle. For instance, an adventurous and outgoing speaker is more likely to make it to the conference in time because of his increased experience with all kinds of actions. Similarly, an emeritus professor, who is an active oarsman at the same time, has bigger chances of making it than a young but motor incompetent assistant professor.

Part II

Study I

The dynamics of the interrelation of perception and action across the life span

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Abstract

Successful social interaction relies on the interaction partners' perception, anticipation, and understanding of others' actions. The perception of a particular action and the capability to produce this action share a common representational ground. So far, no study has explored the interrelation between action perception and production across the whole life span using the same tasks and the same measurement techniques. This study was designed to fill this gap. Participants between 3 and 80 years ($N = 214$) observed two multistep actions of different familiarity and then reproduced the according actions. Using eye tracking, we measured participants' action perception via their prediction of action goals during observation. To capture subtler perceptual processes, we additionally analysed the dynamics of gaze behaviour using recurrence quantification analysis (RQA). Action production was assessed via the accuracy of the participants' reproduction of the observed actions. No age-related differences were found for the perception of the familiar action, where participants of all ages could rely on previous experience. In the unfamiliar action, where the participants had less experience, action goals were predicted more frequently with increasing age. The RQA revealed that the recurrence in gaze behaviour was related to both, age and action production: Gaze behaviour was more recurrent (i.e. less variable) in very young and very old participants, and lower levels of recurrence were related to higher scores in action production across participants. Incorporating a life-span perspective, this study illustrates the dynamic nature of developmental differences in the associations of action production with action perception.

Key words: Development; social cognition; dynamic systems; action production; common-coding; recurrence analyses

The dynamics of the interrelation of perception and action across the life span

Our society is built upon the interaction between its members. Successful social interaction relies on the interlocutors' reciprocal perception, anticipation, and understanding of others' behaviour that is often expressed through their observable goal-directed actions (Blakemore & Decety, 2001). Hence, the perception of others' actions (henceforth called *action perception*) builds the basis for the correct interpretation of others' intentions, implicit and explicit goals (Gallese & Goldman, 1998), and facilitates joint action, cooperation, and social learning (Sebanz & Knoblich, 2009).

Therefore, gaining knowledge on the factors influencing action perception is vital. Previous work indicates that action perception is affected by the interlocutors' capability to produce a specific action (Hommel et al., 2001). Furthermore, this accuracy and/or speed in performing a certain action (*action production*) along with action perception undergo substantial developmental changes across the whole life span (Adolph & Berger, 2011; Diersch et al., 2012; Gampe et al., 2015; Houx & Jolles, 1993). However, although evident, the age-related differences in the interrelations between action perception and action production have only been studied within narrow age ranges. Therefore, the aim of the current study was to determine how age-related variations in action production are interrelated with age-related differences in action perception across the human life span. Importantly, to allow for comparisons between the different age groups, action perception and action production were assessed with the same measurement techniques across all age groups (using eye tracking) and one theoretical framework (*dynamic system approach*; Thelen & Smith, 1994) was applied to account for the expected life-span differences.

Commonly, the interrelations between action perception and action production are assumed to be based on a common representational basis of perceived and produced actions (*common-coding approach*; Hommel et al., 2001). In support of this assumption, prior work has found evidence for overlapping cortical processing areas within the sensorimotor system for action perception and action production (Gallese et al., 1996; Grafton, 2009; Iacoboni et al., 1999; Léonard & Tremblay, 2008; Marty et al., 2015). In line with this sensorimotor dependency, previous studies indicate that the accumulated experience with actions (*action experience*; Catmur, Walsh, & Heyes, 2009; Sommerville, Hildebrand, & Crane, 2008) and the observers' general motor competence (Wermelinger, Gampe, & Daum, 2017) influence these interrelations.

Developmental studies suggest that the coupling between action perception and action production skills emerges early in development (Meltzoff & Prinz, 2002). Already in 3-month-olds, active experience with the to be observed action enhanced action perception (Sommerville et al., 2005). Similarly, infants' evaluation (Daum et al., 2011) and anticipation (Ambrosini, Costantini, & Sinigaglia, 2011) of the goal of a grasping action is correlated with their own action production skill. For instance, while simple reaching or feeding actions are anticipated already by 6-month-olds (Kochukhova & Gredebäck, 2010), only at the age of 12 months, infants anticipate the goal of more difficult reach-and-transport actions (Falck-Ytter et al., 2006). On the neural level, the desynchronisation of the mu rhythm is shown to vary with 9- and 12-months-old's action production skill (Cannon et al., 2016; Yoo et al., 2016). This EEG rhythm is recorded over sensorimotor areas and its desynchronisation is associated with action perception and motor activity during action production (Pfurtscheller et al., 1997). Taken together, studies on infants show that action perception, independent of whether it is assessed through action evaluation, action prediction, or the activity of the sensorimotor system correlates with the children's skill to produce and experience with the respective action (Loucks & Sommerville, 2012; Melzer et al., 2012; van Elk et al., 2008).

The interrelations between action perception and action production are not restricted to early stages of ontogenesis. On the behavioural level, adults with a particular motor expertise such as figure skating (Diersch et al., 2013) or tennis (Farrow & Abernethy, 2003) predict the continuation of a movement of their respective expertise more accurately than novices. Also in non-experts, action perception varies with action production skill: When observing video-recordings of their own actions and recordings of other persons' actions, participants were more accurate in predicting the goal of their own actions (Knoblich & Flach, 2001; Knoblich et al., 2002). Additionally, already short motor training in the respective action enhances the accuracy and speed of predicting the action goal (Hecht et al., 2001; Möller et al., 2015). On the neural level, the activity of sensorimotor brain regions during action perception varies with the observers' experience with an action and action production skill (Catmur et al., 2008, 2009; Heyes, 2010; Press et al., 2011). For example, brain areas involved in performing an action were engaged more strongly during the perception of actions for which the observers have a specific motor expertise than for actions for which the participants only possess visual experience (e.g. dancers: Calvo-Merino et al., 2006; volleyball and tennis players: Balser et al., 2014; pianists: Haslinger et al., 2005; Haueisen & Knösche, 2001; biologically possible vs. impossible actions: Stevens, Fonlupt, Shiffrar, & Decety, 2000).

In sum, the reviewed studies indicate that action perception and action production are related across the life span. However, when taking a life-span perspective, the specific form of the relationship may be expected to differ across development. On the one hand, advancing age is assumed to go hand in hand with an accumulation of active experience with different actions. These differences in action experience are associated with variations in the cortical representation of sensorimotor information (Karni et al., 1998; Matsuzaka et al., 2007; Poldrack et al., 2005) and thereupon influence the perception of actions. In line with this, previous studies indicate the life-long differences in action experience to be associated with according differences in action perception across the life span (Catmur et al., 2009; Sommerville et al., 2005). On the other hand, accuracy and speed in the production of particular actions (henceforth called *action production skills*) follow a more inverted U-shaped development: They increase across childhood (Adolph & Berger, 2011) and decrease again in late adulthood (Houx & Jolles, 1993; Kauranen & Vanharanta, 1996). Early in life, in particular in infancy, increasing age is associated with enhanced prospective action control (von Hofsten & Rönnqvist, 1988) and increased accuracy of goal-directed movements (D'Souza et al., 2017; von Hofsten, 2004). Towards the upper end of the life span, in late adulthood, advancing age is characterised by less precise motor planning (Reuter et al., 2015) and reduced sensorimotor control of actions (Seidler & Stelmach, 1995). Importantly, because of their common base, these differences in action production skills across the life span are associated with according differences in action perception. That is, paralleling the increase and decline of action production skill, the prediction of an action goal increases in early childhood (Gampe et al., 2015) and declines in the elderly (Diersch et al., 2012). This decline is associated with differences in activation patterns in the sensorimotor system between younger and older participants (Diersch et al., 2013, 2016). In sum, while studies on motor competence indicate a linear increase of action perception with age, previous work on action production skills suggests a more inverted U-shaped trajectory of action perception across the life span.

So far, no study has explored the development of action perception and action production and their interrelation across the whole life span using the same tasks and the same measurement techniques. The current study was designed to fill this gap in research. To capture such a life-long trajectory, eye tracking was used as measurement technique because it is suitable for children and adults likewise. The study was furthermore embedded in the theoretical framework of the dynamic system approach to account for the dynamics of the interrelation between action perception and action production from a life-span perspective. In the following, we discuss both aspects in more detail.

Theoretically, we embed the present research in the idea that development unfolds in a dynamic and interactive way (Smith & Thelen, 2003). According to this dynamic system approach, life-span development can be understood as a multicausally determined self-organising process (Smith & Thelen, 2003). Observable behaviour results from the dynamic, nonlinear and real-time interaction of various components (e.g., language, memory) on different levels of hierarchy (e.g., neurons, tissues, cortical regions; Thelen & Smith, 1994). Changes in behaviour across development occur when one or more components of such a dynamic system change beyond a certain threshold. That is, while the system shifts from one relatively stable state to another, the interactions between components are destabilised and reorganised. Such phase transitions are characterised by instable states of the dynamic system (Thelen & Smith, 1994) and are more frequent towards the start and the end of the life span (Johnson, 2000; Park & Reuter-Lorenz, 2009). In the current study, we regard action perception as a developmental output of the real-time interaction between various components. The two components that are of particular interest for the present purpose are the participants' age and their action production skill. Other components may involve the participants' physiological characteristics, sensory processing abilities, cortical structures and activation patterns but also situational or motivational aspects. Including these components as well, however, would go far beyond the current study.

With the current study, we investigated the differences in action perception across the life span within such a dynamic system approach (Thelen & Smith, 1994). Using eye tracking, we assessed eye movements of participants between 3 and 80 years during action observation. We adapted a paradigm from Gampe et al. (2015), in which toddlers aged 12 to 30 months observed two manual multi-step actions in which blocks were moved into a box using a tool. The manual movements and the tools differed in their familiarity between the two actions (*familiar* and *unfamiliar* condition). Specifically, the action in the unfamiliar condition was less transparent in its affordance than the action in the familiar condition and consisted of a novel combination of familiar action steps. After observing the action (*action-perception task*), participants were asked to reproduce the observed action with the same objects at their disposal (*action-production task*). The participants' action production skill was assessed via the accuracy of their imitation of the previously observed actions. The findings of the original study indicated a difference in action perception and action production between the two actions with an advantage for the familiar action.

In the current study, we included and compared two measures of action perception. As a more traditional measure of action perception, we calculated the frequency of predictive eye movements to the action goal. Predictive gaze shifts are used to measure action perception in children as well as adults (Falck-Ytter et al., 2006; Flanagan & Johansson, 2003; Gesierich et al., 2008; Melzer et al., 2012). Specifically, Flanagan and Johansson (2003) showed that these predictive eye movements are present during both production and perception of simple goal-directed actions. Similarly, Rosander and von Hofsten (2011) showed that this coupling between gaze and hand movement is already present in 10-month-olds. Furthermore, predictive eye movements are causally related to the recruitment of the observer's motor system during action perception (Elsner, D'Ausilio, Gredebäck, Falck-Ytter, & Fadiga, 2013) and facilitated by prior action experience (Cannon et al., 2012).

However, oculomotor abilities change across the life span (Pratt et al., 2006). For instance, when comparing infants gaze behaviour to those of adults within an action prediction paradigm, the infants made more saccades to reach the action goal and consistently arrived at the action goal later than the adults (Rosander & von Hofsten, 2011). Therefore, action perception as operationalized via age-sensitive measures such as (gaze) latencies may not easily be compared between children and adults. A more idiosyncratic measure of action perception is the characterisation of gaze behaviour time-series. Time-series analyses capture the complexity of the dynamics of behaviour and give insights into more subtle processes involved that are not captured by the relatively global measure of anticipation frequencies. By employing recurrence analysis (as one analysis technique of behavioural time-series) on the participants' gaze behaviour, we explored the relative stability of participants' gaze behaviour as a more covert measure of action perception. Specifically, we investigated whether certain states in gaze behaviour recur over time as a reference of the dynamic system's stability (*recurrence*; Anderson et al., 2013) and, in particular, how this stability changes with respect to age and action production skill. Specifically, higher recurrence rates in participants' gaze behaviour indicate higher stability in the dynamic system.

Taken together, the current study investigates the influence of the skill to produce a specific action on the perception of familiar and unfamiliar actions across the life span. Based on previous findings (Adolph & Berger, 2011; Kauranen & Vanharanta, 1996), we expected the accuracy of participants' action production to follow an inverted U-shaped trajectory across life span. When looking at action perception, we did not expect to find a substantial influence of age or action production skill on the perception of the familiar action, since this action has been shown to already be very familiar to children of 18-30 months of age in the original study (Gampe et al., 2015). In contrast, with respect to the unfamiliar action, we assumed participants' action perception as indicated by anticipation frequencies to either increase linearly with advancing age or to follow an inverted U-shaped trajectory. That is, because participants accumulate action experience across their life span, this could be associated with a paralleled increase action perception. Alternatively, their action perception is influenced by action production skills therefore follows a similar U-shaped trajectory. Moreover, we assumed gaze patterns to be less recurrent towards the upper and lower end of the life trajectory as an indicator of destabilisations within the dynamic system in young children and older adults (Thelen & Smith, 1994).

Methods

Participants

In the current study, $N = 214$ participants evenly distributed across the ages of 3 to 80 years were included (55.5% females). We measured the behaviour of children between 3 and 4 years and 8 and 10 years as well as adolescence between 14 and 16 years and adults between 20 and 80 years into the study. The spacing between age groups was closer in childhood compared to adulthood because we expected changes to manifest themselves faster in younger years. All adult participants reported normal or corrected-to-normal vision.

All procedures were approved by the local research committee and performed in accordance with the ethical standards of the 1964 Helsinki declaration and its later amendments. Participants or their parents (for children until 16 years of age) gave written informed consent. The adults were recruited via mailing lists and public announcements. They received a reward of an approximate value of USD 15 for their participation. Children up to 10 years were recruited from a database of parents who had volunteered to participate in developmental studies with their children. They received a gift worth approximately USD 5 after their participation; no financial compensation was given to the parents. Children between 14 and 16 years were recruited via birth records and were given a cinema voucher (value of approximately USD 15) for their participation. The participants of this study are an age-matched subset of a larger sample to ensure an even distribution of participants across both experimental conditions.

Materials

The materials were adapted from Gampe et al. (2015). In the action-perception task, participants were presented with video recordings of two actions varying in familiarity to the observer (*familiar* and *unfamiliar* condition). In both conditions, the goal of the action was to put four different coloured blocks into the according holes in a box of the same colour using a tool. The boxes (visual angle: 16.1 x 8.1 x 6.5°), blocks, and tools were similar in form and size across the two conditions. However, the two conditions differed in colour of the boxes and blocks as well as type of tool used. While a hammer was used in the familiar condition, the tool in the unfamiliar condition consisted of a lever with a Velcro-covered end that could be attached to a Velcro-covered lever at the box (see Figure 2 for an overview of the materials and actions).

Hence, while the overall goal for both conditions was the same, movements and tools used to achieve the goal differed. Specifically, in familiar condition the blocks were placed on the box on a straight movement path and then hammered into the box. In the unfamiliar condition, the blocks were placed on the box using a rotating end-state comfort movement and an unfamiliar lever tool was used to insert them into the box. Each condition comprised four action sequences, one sequence for each of the coloured blocks. Each action sequence consisted of four action steps: The block was grasped (Step 1), transported and placed on top of the box (Step 2), the tool was grasped (Step 3), and the block was entered into the box using the tool (Step 4). The action sequences for each of the four blocks were later edited to equal length. However, the length of the two conditions differed due to the natural variation in movement (for exact timing see Gampe et al., 2015). The participant’s eye movements were measured using an Eyelink 1000Plus near infrared eye-tracker (SR Research, Canada, sampling rate: 500 Hz) and Experiment Builder Software (SR Research). A 9-point calibration was used for the adults and a 5-point calibration was used for the children. Stimuli were presented on a 17" display. The display as well as the near-infrared lights and the camera were mounted on a movable arm in 60 cm distance to the participant.

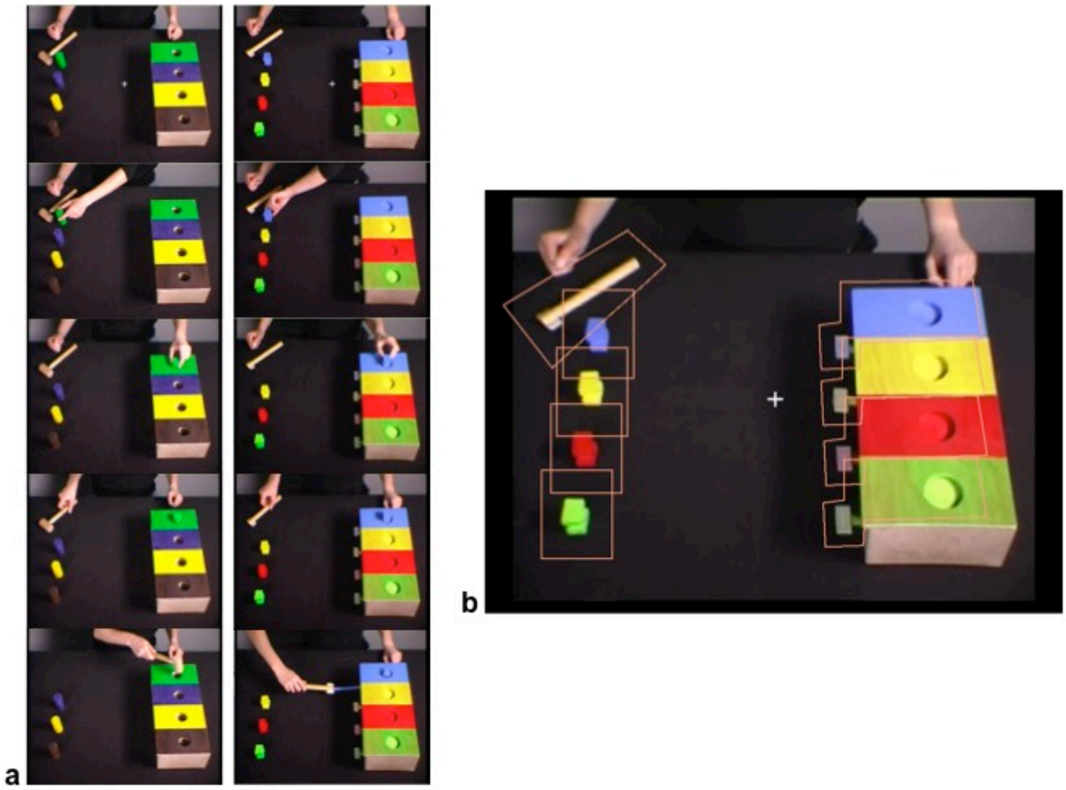

Figure 2. a. Action sequences of the two actions (familiar and unfamiliar). b. The areas of interest (AOIs) were similar to Gampe et al. (2015) and consisted of the action goals of each action step.

Design and procedure

The procedure was held as constant as possible for all age groups. Two exceptions were inevitable. First, for the children (3 to 16 years), the experimental session was preceded by a short familiarisation and instruction phase in the lab's playroom as well as a handedness test. Second, because the adults were tested within a larger project, they had already completed a number of eye-tracking tasks before engaging in the one described in this study (depending on order: 3 to 6 tasks in 10-30 minutes).

The two conditions were presented in a counterbalanced order. Within each condition, the actions were shown three times to the participating children and two times to the adult participants. This was done to ensure that the children had enough opportunities to learn the action sequence for the proceeding action-production task (similar to Gampe et al., 2015). However, adult pilot data suggested transfer effects from one condition to the other (e.g., increases in anticipation frequencies in the second compared to the first condition observed), probably because both actions follow a similar structure. Therefore, and to compare action perception across children and adults, only the first two trials of the first condition presented to every participant were analysed. All further analyses are based on between-subject data. In each condition, the observation of the action recordings was followed by the action-production task of the respective action. The participants were instructed to reproduce the observed action as accurate and as fast as possible with the original materials. Participants' performance in the action-production task was video-recorded.

Data analysis

Action-perception task. The eye-tracking data was processed with the Data Viewer Software (SR Research). The areas of interest (AOIs) were similar to Gampe et al. (2015) and consisted of the action goals of each action step (see Figure 2 for a spatial overlay with the materials presented). For Step 1 the action goals were the blocks (AOI area: 22.3°), for Step 2 and 4 the action goals were the coloured areas on top of the box (AOI area: 34.5°), and for Step 3 the action goals were the two tools (AOI area: 34.3°). The AOI surface was reduced for the recurrence analysis to prevent overlapping of AOIs.

Anticipation frequencies. To obtain the frequency of anticipatory gaze shifts towards the action goal, the difference in time between the arrival of the actor's hand in the respective goal AOI and the participant's first fixation in the same area was calculated (gaze latency) for every action step. To ensure sufficient data quality, only action steps were included in which participants provided valid data for at least half of the total action step duration. Next, for each participant, the number of action steps in which the participant's gaze arrived prior to the actor (predictive gaze shift) were divided by the total number of action steps that passed the quality criterion (predictive and reactive gaze shifts) resulting in an average individual anticipation frequency.

Recurrence analysis. To explore the participants idiosyncratic gaze pattern, we analysed their fixations across the AOIs in intervals of 500 ms. That is, for each interval we assessed whether the participants' eyes were located within one of the goal AOIs (as described above) or within the rest of the display at this point in time. Therefore, the analysis included fixations in AOIs independent of the current location of the currently performed action. The sequence of fixations within the goal areas were indicated with the according AOI and entered into a recurrence analysis (RQA; Zbilut & Webber, 1992) performed with R (R Core Team, 2012). Recurrence analyses have been used previously to describe complex dynamic systems (e.g., climatological data: Marwan & Kurths, 2002; heart-rate variability: Marwan et al., 2002) and to analyse gaze patterns (Anderson et al., 2015, 2013). Recurrence is usually illustrated with recurrence plots (Figure 3). Within these plots, the fixation sequence is plotted with itself over all intervals and re-occurring fixations are represented with recurrent points. Two fixations are considered recurrent if they are close together. In our study, this closeness was defined via the areas of interest. Hence, we considered fixations to be recurrent if they land in the same AOI. The recurrence rate is defined as the percentage of recurrent fixations per fixation sequence. It indicates how often observers re-fixated previously fixated AOIs and whether certain states of the system recurred over time as a reference of the stability of the system. In short, higher recurrence is associated with a more stable state of the dynamic system.

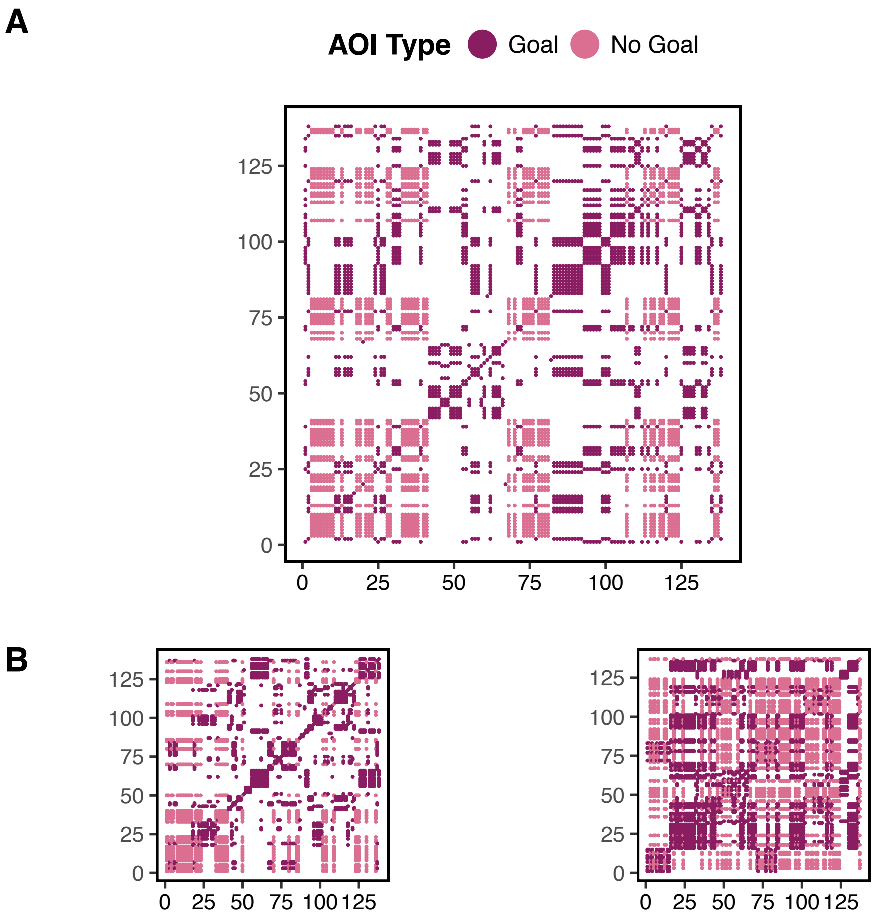

Figure 3. Recurrence is illustrated with recurrence plots. A: Darker recurrence points represent recurrent fixations within the goal AOI's, lighter recurrence points represent fixations within the rest of the display. Recurrence plots are symmetrical around a central diagonal line. This line represents the fixation sequence as it was observed. B: Examples of recurrence plots showing low (left) and high (right) recurrence as indicated by the number of recurrence points.

Action-production task. Performance in the action-production task was coded from video by three different trained coders (κ > .85). For every action step, participants' imitation was compared to the actions presented during the perception task. Actions steps were considered correctly reproduced if they were executed with the correct hand (right hand for block grasp and left hand for tool grasp), if the blocks were transported towards the box on the same movement path (straight in the familiar condition and rotational in the unfamiliar condition), if the colours of the blocks and the box segment matched up, and if the according tools were used to enter the blocks into the boxes. Every multistep action consisted of four action sequences à four action steps. Therefore, the participants' imitation score could take a number between 0 and 16. The imitation score of n = 2 participants in the familiar condition, and n = 2 participants in the unfamiliar condition could not be obtained because of technical problems with the video-recording system.

Results

The results section is divided into three sections. First, we will present the results on the relation of age and action production skill. Second, the association between age and action perception is reported. Within the third section, the data on the interrelation of action perception and action production skill across the life span are presented. In all sections, action perception is operationalized by the anticipation frequencies as a measure of overt behaviour and by recurrence as a measure of covert behaviour. To make scales comparable, all independent variables were z-standardised before being entered into the analysis (see Appendix A1 for zero-order correlations of all variables of interest).

Age and action production skill

Using R (R Core Team, 2012), two polynomial regressions were conducted to analyse the effect of age on imitation score within each condition separately. For the familiar condition, results show significant linear (β = 0.079, SE = 0.013, p < .001) and quadratic effects of age (β = -0.003, SE = 0.001, p < .001). This indicates that participants action production skill followed an inverted U-shaped form across the life span, $F(2,102) = 25.330$, p <.001, R^2 = .332, indicating a more precise action production in young and middle-aged adults compared to young children and old adults. The same results pattern was found for the unfamiliar condition, $F(2,102) = 14.410$, p <.001, R^2 = .220. Again, the results yielded a significant linear (β = 0.052, SE = 0.012, p < .001) and a significant quadratic association of age and imitation score following the same inverted U-shaped pattern as reported before (β = -0.003, *SE* = 0.001, $p < .001$; Figure 4 and Appendix A2).

Age and action perception

Anticipation frequency. We conducted two separate linear regressions of age on the anticipation frequencies in the two conditions (Figure 4). In the familiar condition, age was not associated with the participants' anticipation frequency, $F(1,105) = 0.362$, $p = .549$. In the unfamiliar condition, the more parsimonious linear model, $F(1,105) = 7.153$, $p = .009$, $R^2 = .064$, yielded the same fit ($p = .129$) with the data like a quadratic model, $F(2,104) = 4.793$, $p = .010$, $R^2 = .084$. Accordingly, the linear model was employed, which indicated that in the unfamiliar condition, participants predicted more action steps with increasing age (β = 0.002, *SE* = 0.001, $p = .009$; see Appendix A2 for details of regression analyses).

Recurrence. Two linear regression analyses of age on recurrence were conducted for each condition separately (Figure 4). The results show no effect of age on the recurrence in the familiar condition, $F(1,105) = 1.083$, $p = .300$. In the unfamiliar condition, a linear model, $F(1,105) = 2.332$, $p = .130$, fit the data less ($p = .003$) than a quadratic model, $F(2,104) = 5.878$, $p = .004$, $R^2 = .102$. That is, fixations were less recurrent in young children and in older adults compared to adolescents, young and middle-aged adults (linear: β = 0.000, *SE* = 0.000, $p = .014$; quadratic: β = -0.000, *SE* = 0.000, $p = .003$; see Appendix A2 for details of regression analyses).

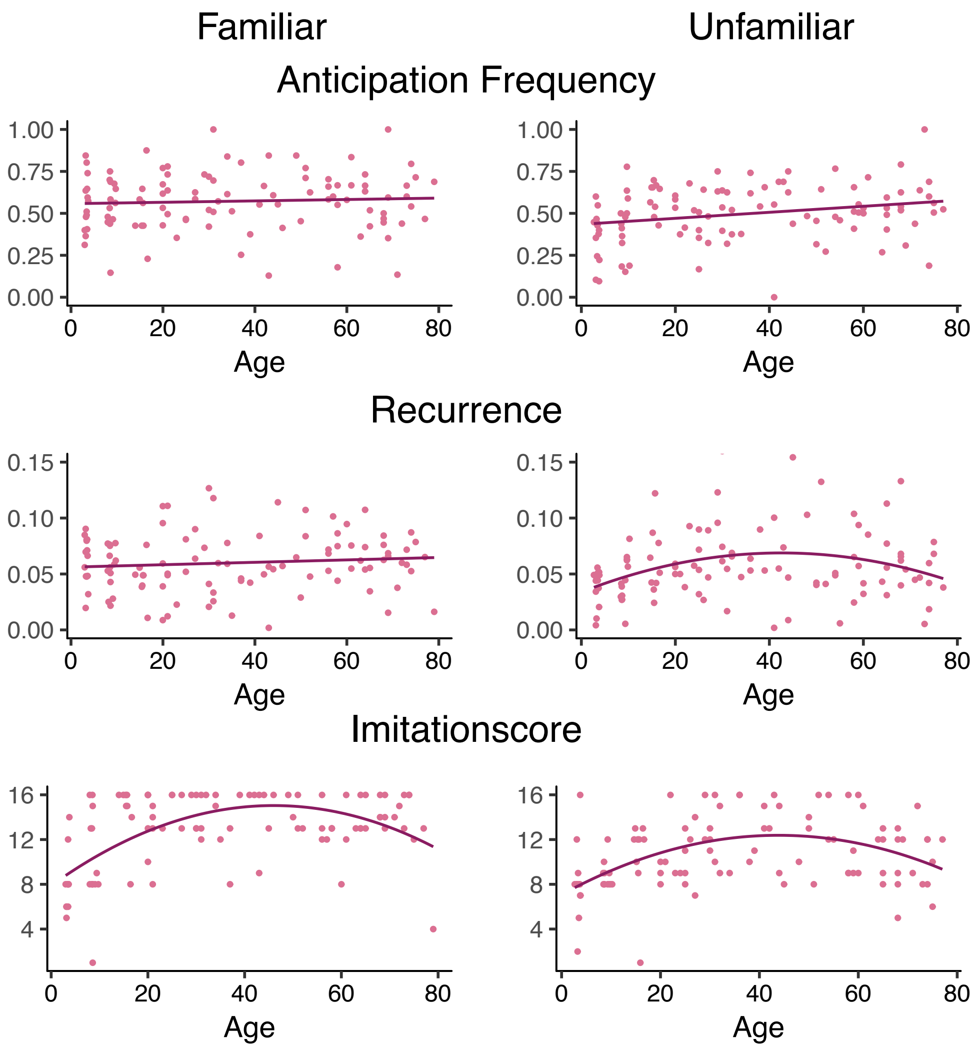

Figure 4. Relationship between age and anticipation frequency, recurrence, and imitation score for the familiar (left) and the unfamiliar action (right).

Action production skill and action perception across the life span

Anticipation frequency. For each condition, we explored the association of participants' imitation score and their anticipation frequency and investigated whether age moderates this relationship. Two linear regressions with imitation score, age, and their interaction on anticipation frequency were conducted. In the familiar condition, the results showed no associations between imitation score and anticipation frequency, $F(3,101) = 0.209$, $p = .890$. In the unfamiliar condition, the regression model, $F(3,101) = 2.761$, $p = .046$, $R^2 = .076$, yielded no significant association of imitation score with anticipation frequency (β = 0.001, *SE* = 0.005, *p* = .848). Furthermore, a significant effect of age (β = 0.002, *SE* = 0.001 *p* = .008) but no interaction between imitation score and age (β = 0.000, *SE* = 0.000 *p* = .750) emerged. Hence, older participants predicted action steps of the unfamiliar action more frequently than younger participants independent of their imitation score (see Appendix A4 for details of regression analyses).

Recurrence. Similarly, the association of participants' imitation score and recurrence as well as a possible moderating effect of age were explored for the two conditions separately. Two separate regressions of age and imitation score, and their interaction on recurrence were conducted. In the familiar condition, the results show showed no significant associations, $F(3,101) = 1.208$, $p = .311$. However, in the unfamiliar condition, a quadratic model, $F(5,99) = 4.722$, $p < .001$, $R^2 = .193$, indicated a significant linear association of imitation score (β = -0.003, *SE* = 0.001, *p* = .041), as well as a linear (β = 0.000, *SE* = 0.000, *p* = .010), and a quadratic association of age (β = -0.000, *SE* = 0.000, *p* < .001) with recurrence. No interaction between imitation score and age emerged (linear: β = -0.000, *SE* = 0.000, *p* = .055; quadratic: β = 0.000, *SE* = 0.000, *p* = .814). Hence, in the unfamiliar action, high imitation scores were related to less recurrent gaze behaviour independent of age (see Appendix A4 for details of regression analyses).

Discussion

The current study explored the association of individual's particular capability to produce a specific action with their perception of goal-directed actions across the life span. To this end, participants from 3 to 80 years observed a familiar or an unfamiliar action and thereupon were asked to imitate the according action. Action perception was measured via the participant's prediction of the action goal as well as the recurrence of their gaze behaviour during the observation of the actions. Action production skill was measured via the closeness of participant's imitation of the observed action. The results showed no relationship between age and action perception – measured via anticipation frequency and recurrence – in the familiar condition. Similarly, the participants' action production skill was not associated with their action perception for the familiar action. In contrast, when observing unfamiliar actions, anticipation frequencies linearly increased with age. Furthermore, participants' gaze behaviour was less recurrent at both ends of the age spectrum in the unfamiliar condition. When looking at relationship of action production skill and action perception across the life span, no association was found for anticipation frequencies. However, participants with a high imitation score were less recurrent in their gaze behaviour in the unfamiliar condition across the life span. In sum, our results indicate that action perception differs across the life span. These differences vary with the familiarity of the action to the observer and his or her accuracy in imitating the according action. In the next paragraphs, we will discuss the life-span trajectories of these interrelations separately for our two measures of action perception applied (anticipation frequency and recurrence).

Anticipation frequency across the life span

Anticipation frequency linearly increased with age for the unfamiliar action. This is in line with previous studies suggesting that life-long, accumulated action experience changes how actions – produced or perceived – are processed (Diersch et al., 2013; Falck-Ytter et al., 2006; Knoblich & Flach, 2001; Loucks & Sommerville, 2012; Melzer et al., 2012). However, studies with both infant and adult participants (Cross et al., 2006; van Elk et al., 2008) also showed that it takes a considerable amount of experience with a certain action before this has an impact on action perception. In line with this, we still found an increase of anticipation frequency with advancing age in the unfamiliar condition while there was no effect of age in the familiar condition. Hence, while the familiar action was already familiar enough to the youngest participants to be anticipated with a relatively high frequency, the accumulated action experience over age was beneficial when it came to predicting the action goals of the unfamiliar action. This is in line with previous studies indicating a change in sensorimotor activity during action observation before and after experience with the according action (Gardner, Aglinskas, & Cross, 2017; Gardner, Goulden, & Cross, 2015).

Recurrence across the life span

Similar to our findings on anticipation frequencies, participants' age affected recurrence only in the unfamiliar, but not in the familiar condition. The analysis of the time-series of participant's gaze behaviour allows capturing the complexity of dynamical systems such as life-span development in more detail than the relatively rough measure of anticipation frequencies. In this connection, more stable phases of dynamic systems are accompanied with increased predictability of behaviour (as indicated by high recurrence rates), while reorganizational processes within the system during instable phases (as indicated by low recurrence rates) lead to less predictable and highly variable behaviour (Thelen & Smith, 1994). In the current study, the participants' gaze behaviour was less recurrent at the two ends of the age spectrum within the unfamiliar condition – indicating less stable states. Therefore, we assume the development of action perception to undergo periods of transition in childhood, stabilisation in adulthood and destabilisation later in life, which are observable in the differences in the recurrence in gaze behaviour.

This assumption finds support in other theoretical frameworks on life span development. For instance, the interactive specialization approach (Johnson, 2000, 2001) assumes neural structures to be activated via multiple pathways and different stimuli in early phases of development. Through dynamic changes on the structural and functional level of cortical networks (e.g., pruning or inhibition of unused associations) these response properties become more specialized and cortical regions more selectively activated by certain kinds of stimuli. On the other end of the life span, the Scaffolding Theory of Aging and Cognition (STAC; Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) states that the brain seeks to maintain a delicate equilibrium while facing external (e.g., unfamiliar situations) and internal (e.g., aging) changes. This equilibrium is established through a constant reorganisation of the brain (e.g., strengthening of existing pathways, establishing new pathways or inhibiting ineffective connections). Together, these lines of thinking assume a dynamic and flexible cortical organisation across development and predict an increasingly narrower response pattern with increasing age during childhood and an again broadening of response patterns towards late adulthood.

The interrelation between action perception and production skill across the life span

In contrast to previous studies (Ambrosini et al., 2011; Kirsch & Cross, 2015), the accuracy of action production was not associated with action perception as indicated by anticipation frequency (for both actions). We suggest, that the assessment of action perception via the frequency of predictive eye movements might be a too global measure that is not sensitive enough to capture subtle developmental processes (Thelen & Smith, 1994). In line with this, the recurrence of the participants' fixation sequence as more covert measure of action perception did show a significant association with the imitation score for unfamiliar action: Participants with higher imitation scores showed lower recurrence in their gaze behaviour. While this might seem surprising at first sight, one has to keep in mind that we measured the recurrence of fixations within the goal AOIs. Learning a new action involves monitoring the scene and paying close attention to the exact kinematics of the movements used to reach the action goal (Hayes, Roberts, Elliott, & Bennett, 2014; Sumanapala, Fish, Jones, & Cross, 2017). That is, to successfully reproduce the observed actions, the participants had to look at the agent's hand moving the blocks or the tool in the areas between the AOIs. Therefore, the recurrence of the fixation sequence within the action goal AOIs is likely to be negatively associated with the accuracy of action production

Furthermore, having a specific expertise in action production was associated with action perception independently of age. This is in line with previous research showing a perception advantage for older movement experts compared to equally old non-experts (Diersch et al., 2013, 2012). Even more, the older experts in these studies showed a comparable action perception and sensorimotor activation to young non-experts. In contrast to the results in the unfamiliar condition, we did not find an effect of action production skill on the recurrence in the familiar condition. Since the dynamic system already resided in a relatively stable state for the perception of familiar actions, differences in one subcomponent such as the accuracy in producing the action may not elicit an observable effect.

The exploration of life span development has to be based on theoretical frameworks and measurement techniques, which are suitable for various age groups. The current study addressed these two issues by employing time-series analyses on gaze data and describing life-span development within a dynamic system approach (Thelen & Smith, 1994). This approach makes comparable predictions to other developmental frameworks such as the interactive specialization approach (Johnson, 2000, 2001) and the STAC (Park & Reuter-Lorenz, 2009; Reuter-Lorenz & Park, 2014) and accounts for developmental processes across the whole life span. Moreover, the use of eye-tracking technology and the analysis of gaze time series seem to be a promising route in future life-span research since it gives insights in more covert processes. However, our study was based on cross-sectional data. We did not describe life-span development but only reported differences between age groups instead. Therefore, longitudinal studies are needed to give an appropriate picture of age-related influences on action perception.

With this study, we showed that action production skills are associated with action perception across the life span. Our results suggest that the development of the interrelations of action perception and production is to be seen within a dynamic system framework and does not follow linear pathways.

Study II

Interference of action perception on action production increases across the adult life-span

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Abstract

Action perception and action production are assumed to be based on an internal simulation process that involves the sensorimotor system. This system undergoes changes across the life span and is assumed to become less precise with age. In the current study, we investigated how increasing age affects the magnitude of interference in action production during simultaneous action perception. In a task adapted from Brass et al. (2000), we asked participants (aged 20 – 80 years) to respond to a visually presented finger movement and/or symbolic cue by executing a previously defined finger movement. Action production was assessed via participants' reaction times. Results show that participants were slower in trials in which they were asked to ignore an incongruent finger movement compared to trials in which they had to ignore an incongruent symbolic cue. Moreover, advancing age was shown to accentuate this effect. We suggest that the internal simulation of the action becomes less precise with age making the sensorimotor system more susceptible to perturbations such as the interference of a concurrent action perception.

Keywords: action simulation; sensorimotor system; motor performance; ageing; imitation inhibition

Interference of action perception on action production increases across the adult life-span

Be it during a football game, while driving a car, or in the middle of a conversation: We constantly perceive actions of others while producing different actions ourselves. This perception of others actions is not independent of our own action production. Quite the contrary, action perception and production affect each other reciprocally, in particular, when performed simultaneously: While incongruent action perception and production interfere with each other, the opposite is true for congruent perception and production (e.g., Brass, Bekkering, & Prinz, 2001). In the current study, we investigated how age is related to the interference effects in simultaneous incongruent action perception and action production.

Action perception is modulated by a concurrent action production resulting in interference effects in case perceived and produced actions do not conform (Jacobs & Shiffrar, 2005; Kilner et al., 2003). For instance, Hamilton, Wolpert, and Frith (2004) asked participants to lift boxes of different weights and at the same time make judgments about the heaviness of objects lifted by another actor. The objects lifted by another person were judged to be lighter when the participants themselves lifted a heavy box and heavier when the participants lifted a light box. In the same vain, a congruent action production (e.g., evaluation of movement durations: Hecht, Vogt, & Prinz, 2001; discrimination of hand postures: Miall et al., 2006) facilitates simultaneous action perception. Furthermore, facilitation (Edwards et al., 2003; Ménoret et al., 2013) and interference effects (Brass, Zysset, et al., 2001; Wohlschläger & Bekkering, 2002) are found in the opposite direction, from perception on production. For instance, Hardwick and Edwards (2012) asked participants to execute finger movements while observing an experimenter executing spatially congruent or incongruent finger movements. The participants showed reduced spatial error in their own movement if the perceived action was congruent with their own action (facilitation effect) but increased spatial error if the perceived action did not match with their own action production (interference effect; also see Press, Bird, & Heyes, 2005; Press, Bird, Walsh, &

Heyes, 2008; Press, Gillmeister, & Heyes, 2007).

The simulation theory (Jeannerod, 2001; for a review see Pezzulo et al., 2013) accounts for these interrelations between action perception and action production by stating that, in addition to the overt and observable stage of action, there is another–covert–stage of action. This simulation involves aspects of the future such as the goal of the action, the means to reach it or the consequences of the action (Jeannerod, 2001) without an overt action production. Furthermore, the production, perception, or imagination of an action are assumed to automatically elicit an internal simulation of the latter. Consequently, in cases in which the simulations associated with perception and production differ, they may interfere with each other. More precisely, since the sensorimotor system is already tuned in for a certain action when perceiving it, the concurrent production of an incongruent action interferes with this movement preparation (Blakemore & Frith, 2005).

In line with this assumption, the sensorimotor system is shown to be involved in the internal simulation process (Stadler et al., 2012). For instance, studies using transcranial magnetic stimulation (TMS) during action perception have shown a modulation of the motor corticospinal excitability in accordance with the perceived actions (Aglioti et al., 2008; Fadiga et al., 1995; Gangitano et al., 2001; Urgesi et al., 2006; Valchev et al., 2017). In these studies, the relative sensitivity of the corticospinal tract during action perception was assessed via changes in the threshold needed to evoke responses in the effector muscles while stimulating the motor cortex. Results show a selective increase in the motor-evoked potentials (MEP) recorded from muscles normally used to produce the observed actions (D’Ausilio et al., 2014; Fadiga et al., 1995). Hence, during action perception, the activity of the sensorimotor system, as indicated by the corticospinal excitability, is highly selective for the effector that is involved in action production (D’Ausilio et al., 2009).

However, while this is true in young adults, Léonard and Tremblay (2008) have shown that the corticomotor facilitation is less specialized in older than younger adults during action production, perception and imagination. Furthermore, studies using imaging techniques (Diersch et al., 2013, 2016; Mouthon et al., 2016; Nedelko et al., 2010) have shown that older compared to younger adults activate additional visual and sensorimotor regions during action perception. Hence, age-related de-differentiation and compensation processes with advancing age (Cabeza, 2002; Reuter et al., 2015) might lead to a less precise internal representation and simulation of the actions perceived and produced.

Supporting this notion, the sensorimotor system undergoes age-related changes (Heuninckx et al., 2005; Sharma & Baron, 2014; Ward, 2006; Ward & Frackowiak, 2003). On the behavioural level, these changes result in greater movement variability, general slowing of movements and coordination deficits with increasing age (Seidler et al., 2010). In action production, increasing age is accompanied by less precise motor planning (Reuter et al., 2015), less interhemispheric inhibition (Talelli, Waddingham, Ewas, Rothwell, & Ward, 2008), and reduced sensorimotor control of actions (Seidler & Stelmach, 1995). With respect to action perception, the accuracy of action prediction (Diersch et al., 2012), imagination (Personnier, Kubicki, Laroche, & Papaxanthis, 2010; Personnier, Paizis, Ballay, & Papaxanthis, 2008; Saimpont et al., 2010; Skoura et al., 2005), and the perception of the personal action range (Gabbard, Caçola, & Cordova, 2011) decreases from younger to older adults.

Taken together, the current study is based on the following presumptions: First, action perception and production are interrelated because they are both based on an internal simulation process involving the sensorimotor system (Jeannerod, 2001). Second, along with age-related changes in the sensorimotor system, the precision of this internal simulation process changes over age, and particularly decreases during the adult life span. This becomes evident in changes in action perception and production on the behavioural and neural level. What remains unclear is whether and how increasing age affects the interrelations of action perception and action production as indicated by interference and facilitation effects.

Specifically, the less precise internal action simulation might lead to stronger interference in concurrent action perception and production in older participants. That is, if the sensorimotor system is challenged with two concurrent and contradicting simulation processes, action production should be interfered more by action perception with advancing age. Hence, in the current study we aimed to explore whether the dependence of our own action production on the perception of other's actions differs between age groups or stays constant across the life span.

To address our research question, we adapted a reaction-time task introduced by Brass, Bekkering, Wohlschläger, and Prinz (2000) and applied it to participants between the ages of 20 to 80 years. In the original task, the participants were asked to perform finger movements, which were either congruent or incongruent with finger movements or symbolic cues. The authors reported facilitation (shorter reaction times in participants' finger movements) for congruent trials and interference (longer reaction times) in incongruent trials compared to baseline trials. Importantly, interference effects were more pronounced when the participants observed an incongruent action (i.e. a finger movement) than when they observed an incongruent symbolic cue.

In accordance with Brass et al. (2000), we asked our participants to respond with an index- or middle-finger movement to a visually presented index- or middle-finger movement, or to the appearance of a symbolic cue ("spatial condition" in Brass et al., 2000). The finger movement and symbolic cue could either be congruent, implying the same response finger, or incongruent, implying a different response finger. Previous findings indicate that finger movements, like they were presented in our study, are perceived as goal-directed actions (Bertenthal, Longo, & Kosobud, 2006). Based on the findings reported by Brass et al. (2000), we assumed longer reaction times in response to incongruent trials. In accordance with the simulation theory, this interference was assumed to be larger in trials, in which the participants' action production was interfered by an incongruent action perception. Thus, we expected reaction times to be longest in trials, in which participants were asked to respond to the symbolic cue and ignore the simultaneously presented finger movement. Furthermore, in accordance with Brass et al.'s (2000) findings, we expected reactions times to be reduced in congruent trials if participants were asked to respond to the symbolic cue (facilitation effect). Looking at the effect of age on this pattern, we expected older compared to younger participants to show longer reaction times independent of condition (Houx & Jolles, 1993). Furthermore, older participants were expected to be interfered more in the incongruent trials (Houx, Jolles, Vreeling, & Jolles, 1993; West, 1996). Finally, based on studies indicating a less precise action simulation (Diersch et al., 2016) and the activation of additional areas in older compared to younger adults (Mouthon et al., 2016), we expected older participants to be especially interfered in their action production in the presence of simultaneous action perception (motor interference). Furthermore, increasing age is associated with a decrease in health (Brazier et al., 1992) and the ability to inhibit an automatic response tendency (Korsch et al., 2014; Korsch, Frühholz, & Herrmann, 2016). Both factors were likely to influence the results and were therefore included as control measures.

Methods

Participants

In the current study, the reaction times of $N = 171$ participants between the ages of 20 to 80 years were assessed. From this sample, $n = 157$ participants (Table 1), who passed the quality criterion of at least 10 valid trials per trial type and finger (see Data analysis), were included into further analysis. All participants reported normal or corrected-to-normal vision. All procedures were approved by the local research committee and in accordance with the ethical standards of the 1964 Helsinki declaration and its later amendments. All participants gave written informed consent. They received a reward of an approximate value of USD 30,- for their participation.

Table 1

Participant Characteristics

Age Group (years)	*n*	Gender (*n* female)	Handedness (*SD*)	Education (*SD*)
20-29	26	16	40.01(58.76)	4.23(1.37)
30-39	31	25	73.42(39.22)	5.46(1.57)
40-49	23	11	81.84(27.74)	5.90(1.66)
50-59	27	18	55.02(41.79)	4.78(2.06)
60-69	32	20	80.15(40.46)	4.61(2.00)
70-80	18	8	81.36(38.29)	4.61(1.79)

Note. Characteristics of participants that passed the quality criterion and remained in sample (participants excluded per decade: 30-39: $n = 1$, 40-49: $n = 3$, 50-59: $n = 2$, 60-69: $n = 3$, 70-80: $n = 5$). Means and standard deviations are reported for handedness and education. Handedness (% right) was assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). Highest education is reported in a score ranging from 1 = High School to 7 = University. The education level did not differ between decades, $F(1,148) = 0.31$, $p = .581$.

Procedure

The current study is part of a larger longitudinal research project on the interrelations of action perception and production throughout adulthood. The tasks employed in this project were designed to assess participants' oculomotor skills (e.g. smooth pursuit, saccade velocity), their action perception (operationalized via the prediction of the action goals) and their accuracy and speed in action production. Furthermore, several control measures such as the participants' health status, handedness, motor or cognitive skills were included. Some of these control measures were used for this study. Specifically, the participants' health status was measured with the RAND 36-Item Health Survey (Hays, Sherbourne, & Mazel, 1993). This self-administered survey instrument assesses the health-related quality of life with 36 items. It fulfils criteria for reliability and validity across the life span (Brazier et al., 1992) and discriminates reliably between healthy and unhealthy participants (Hays & Morales, 2001). All participants received the survey in an online version one week prior to the lab session. Participants' inhibition of an automatic response tendency was measured via a Go/noGo task of the Tests of Attentional Performance (TAP; Zimmermann & Fimm, 2012). In this task, the participants were asked to respond to a centrally presented cross ("x") with a button press and ignore a centrally presented plus sign ("+"). Participants' reaction times in this task were assessed in the lab session prior to the reaction-time task.

For this reaction-time task, we adapted an interference task introduced by Brass et al. (2000). Like in Brass et al.'s task, participants were asked to execute finger movements in response to a visually presented finger movement or a symbolic cue. Stimulus delivery and data acquisition were achieved by means of the program Experiment Builder (SR Research, Canada). Stimuli were presented on a 17" display placed in a 60 cm distance to the participant. To record participants' reaction times (RTs), their dominant hand rested on a keyboard with the index and the middle finger on two different keys (index finger: "N"; middle finger: "M"). Task instructions were given prior to the experiment and were repeated right before each block of trials. Participants were asked to execute their finger movements as quickly as possible.

Stimuli

Each trial of the reaction-time task consisted of a sequence of five frames (17.98 ° x 20.75 ° visual degrees; Figure 5a). The sequence started by showing a male hand resting on a black surface with the index and the middle finger elevated. The hand was positioned to appear as a mirror image of the participant's dominant hand (according to Oldfield, 1971). This initial frame was identical for all stimuli and remained visible for 560 ms. Depending on the trial type, the next three frames presented a finger movement, a symbolic cue, or both. The overall displacement of the finger movement presented was 6.95 ° for the middle finger and 8.07 ° for the index finger. The symbolic cue "x" appeared on the fingernail of the corresponding finger. Each frame of this middle section was presented for 40 ms. The presentation of the fifth frame lasted for 520 ms and showed the hand in its final resting position. The total duration of each trial was 1'200 ms. Between the trials, a fixation cross was shown for 1'840 ms.

Design

The frame sequences in the reaction-time task were presented in two experimental conditions. The order of these two blocked conditions was counterbalanced between the participants. In the symbolic condition, the participants were asked to execute an index-finger movement in response to the presentation of a symbolic cue on the index finger and to respond with a middle-finger movement to the presentation of a symbolic cue on the middle finger. Hence, the relevant stimulus dimension in the symbolic condition was the symbolic cue. In the movement condition, participants executed an index-finger movement in response to an observed index-finger movement or a middle-finger movement in response to an observed middle-finger movement. In this condition, the observed finger movements served as the relevant stimulus dimension.

Within these two conditions, trials were presented as baseline trials, congruent trials or incongruent trials (Figure 5b). In baseline trials, the presented stimuli varied only on the relevant stimulus dimension. That is, baseline trials presented in the symbolic condition showed a fixated hand with the symbolic cross appearing on either the index or the middle finger. In the movement condition, participants observed the movement of the index or the middle finger without the additional appearance of the symbolic cue. In the congruent trials of both conditions, the symbolic cue appeared on the fingernail of the moving finger. In the incongruent trials, the finger that moved differed from the finger on which the symbolic cross appeared. Each condition consisted of 72 trials (24 baseline trials, 24 congruent trials, and 24 incongruent trials). Baseline, congruent, and incongruent trials were randomly distributed within each condition. Both conditions started with the presentation of five training trials. The training trials were excluded from all further analyses.

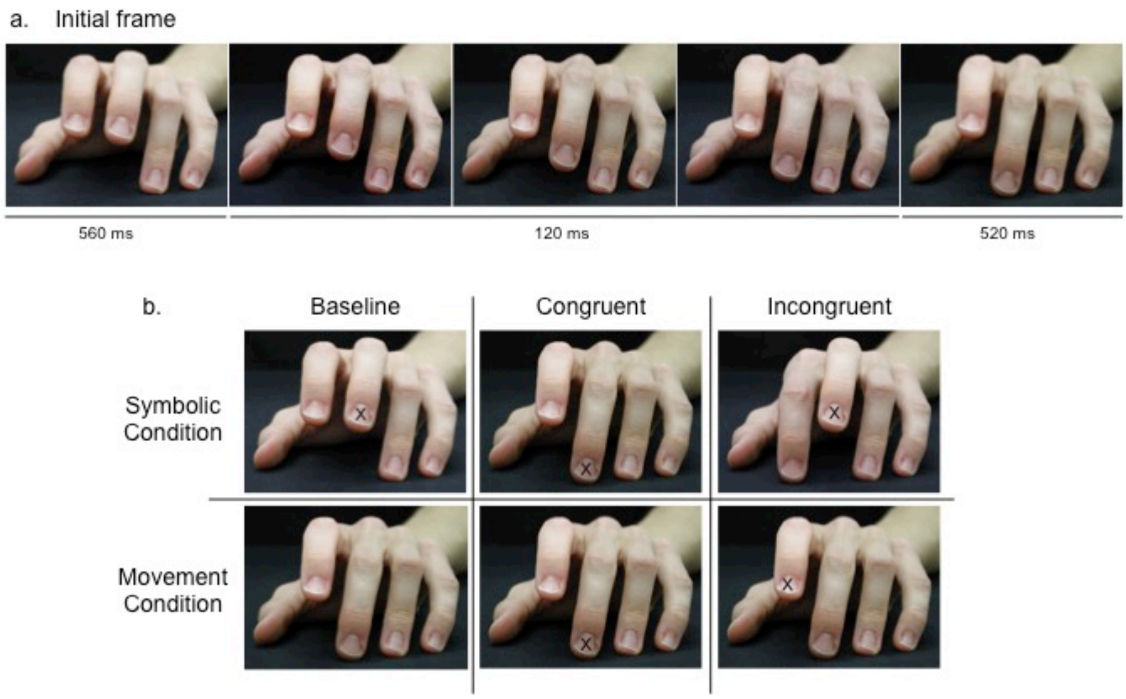

Figure 5. a. Sequence of pictures presented to the participants. b. Sample pictures for the different trials (baseline, congruent and incongruent) per condition (symbolic or movement).

Data analysis

Participants' RTs in the reaction-time task were calculated with respect to the second frame of the stimulus sequence of each trial. The interference between action perception and action production was indicated via the difference in baseline-corrected incongruent trials between the two conditions. This baseline correction was employed to make sure that the differences in interference scores between participants were not attributable to the individuals' differences in their baseline reaction times. Therefore, reaction times in the incongruent trials were corrected for baseline reaction times by dividing the RTs in the incongruent trials of one condition by the RTs in the baseline trials of the same condition. Next, this proportion in the movement condition was subtracted from the proportion in the symbolic condition. This motor interference score represents the influence of action perception on the simultaneous action production, controlled for the visual input and the effect of a second task. Positive values of the motor interference score represent stronger interference in the symbolic condition whereas negative values are associated with a stronger interference in the movement condition. The same score was calculated for the congruent trials.

Trials in which the participants pressed the wrong key were coded as errors and excluded from all further analysis. The mean error rate was 0.75% (SD = 2.89). To ensure sufficient data quality, only participants with at least 10 (out of 12) trials per trial type (baseline, congruent, incongruent) and finger were included in the analysis. This resulted in the exclusion of n = 14 participants (mean age: 60.00 years).

Results

The results section is divided into two parts: First, we present the differences between the reaction times in the two conditions and the three trial types across age. Furthermore, we take a closer look at the incongruent trials of both conditions and compare the interference associated with them. Second, we explore the effect of age on these result patterns.

Differences between conditions and trial types

To replicate previous findings (Brass et al., 2000), we compared the reaction times in the two conditions (symbolic and movement) and the three trial types (baseline, congruent, and incongruent) across age. A 2 conditions x 3 trial types x age repeated measures ANOVA with a Greenhouse-Geisser correction determined that the reaction times differed across conditions, $F(1,155) = 34.74$, $p < .001$, $\eta^2 = .02$, trial types, $F(2,310) = 253.91$, $p < .001$, $\eta^2 = .04$, and age, $F(1,155) = 74.18$, $p < .001$, $\eta^2 = .29$. Furthermore, significant interaction between condition and trial type, $F(2,310) = 29.12$, $p < .001$, $\eta^2 = .01$, age and condition, $F(1,155) = 7.06$, $p = .009$, $\eta^2 = .01$, age and trial type, $F(2,310) = 3.83$, $p = .023$, $\eta^2 = .00$ and a three-way interaction between age, condition and trial type, $F(2,310) = 17.22$, $p < .001$, $\eta^2 = .00$, emerged. To explore these results in more detail, post-hoc tests using Bonferroni correction were performed.

The participants' reaction times in baseline trials did not differ between the two experimental conditions (symbolic and movement), $p = .159$. In the symbolic condition, the reaction times in congruent ($p < .001$) and incongruent ($p < .001$) trials differed significantly from baseline trials. Furthermore, the participants' reaction times in congruent and incongruent trials were significantly different from each other, $p < .001$ (Figure 6a). Thus, in the symbolic condition participants were faster in pressing the correct key when they were presented with a symbolic cue without an additional finger movement than when two cues (finger movement and symbolic cue) were presented simultaneously. In the movement condition, only the participants' reaction times in incongruent trials differed from baseline trials ($p < .001$). The reaction times in congruent and incongruent trials were significantly different from each other, $p < .001$ (Figure 6b). Hence, the participants showed the longest reaction times when the movement of the finger and the symbolic cue contradicted each other.

Taken together, in both conditions, participants' RTs were slower when symbolic cue and finger movement contradicted each other. To explore this finding further, we performed a dependent t-test on the difference score between the RTs in incongruent and congruent trials of both conditions. Results show that this difference score differed between the two conditions, $t(156) = 2.84$, $p = .005$, $r = 0.22$. The difference between incongruent and congruent trials was larger in case the participants had to ignore the irrelevant finger movement (symbolic condition; $M_{diff} = 28.72$ ms, $SD = 29.26$ ms) than when they had to ignore the irrelevant symbolic cue (movement condition; $M_{diff} = 20.13$ ms, $SD = 23.7$ ms).

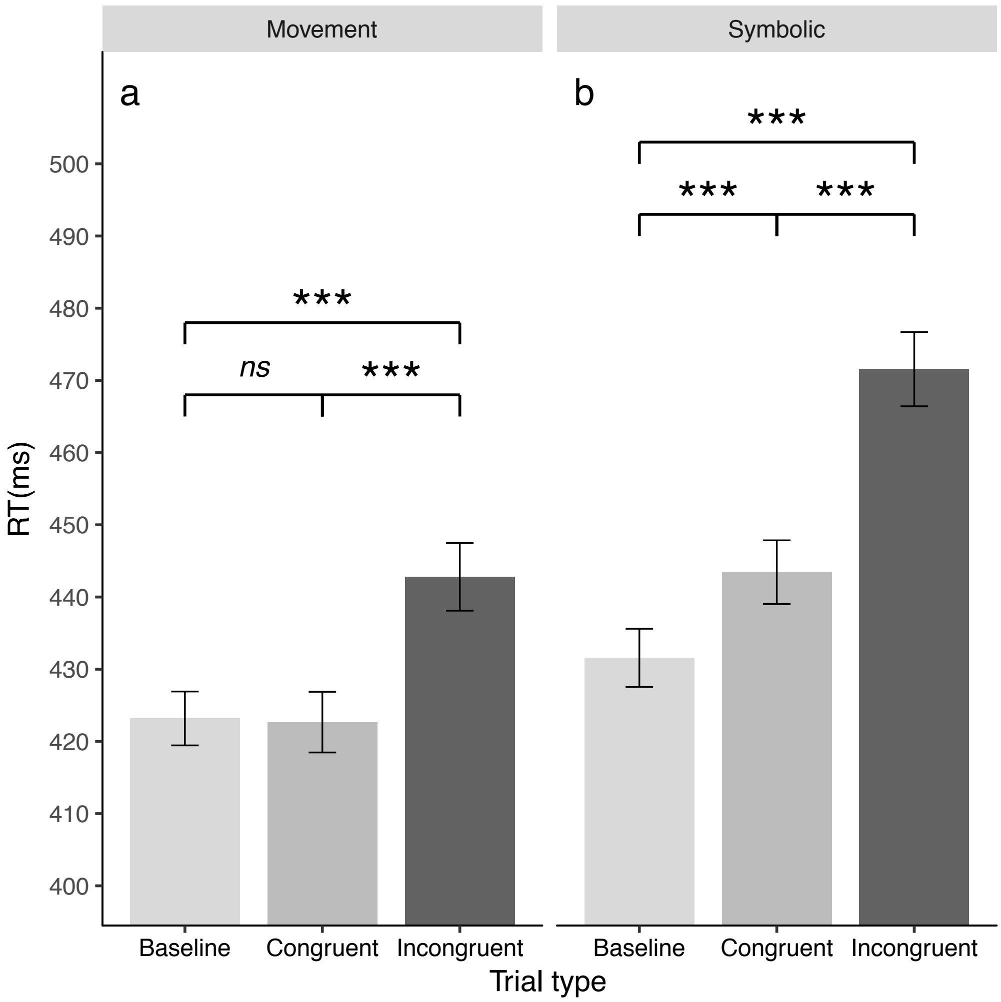

Figure 6. Means and standard errors of reaction times (RTs) in the two experimental conditions (a. movement; b. symbolic) and all three trial types (*** $p < .001$; *ns* = non-significant).

Influence of age

Since our first analysis indicated an effect of age and an interaction of age with condition and trial type, we took a closer look at these age-related influences. Specifically, we explored age-related differences in the interference of action perception on action production. For this, a motor interference score was calculated as described above. Positive values of the motor interference score represent stronger interference in the symbolic condition whereas negative values are associated with a stronger interference in the movement condition.

A linear regression of age on this motor interference score controlling for order of conditions, health status and inhibition was performed. This model significantly predicted the motor interference score, $F(4,143) = 7.70$, $p < .001$, $R^2 = .18$. Only age (β = 0.002, *SE* = 0.000, $p < .001$), but not order (β = -0.006, *SE* = 0.013, $p = .633$), health status (β = -0.000, *SE* = 0.000, $p = .390$) or inhibition (β = -0.000, *SE* = 0.000, $p = .119$), were associated with motor interference. To explore this effect in more detail, we performed two separate linear regressions of age on the RTs in incongruent trials in both conditions. Supporting our initial analysis, the results showed that age significantly predicted the RTs in incongruent trials of the symbolic condition, $F(1,155) = 15.23$, $p < .001$, and in incongruent trials of the movement condition, $F(1,155) = 7.03$, $p = .009$. Importantly, the effect of age was greater in the symbolic condition, $R^2 = .09$, compared to the movement condition, $R^2 = .04$ (Figure 7). This result pattern was unique to incongruent trials and a similar interference score calculated for the congruent trials was not associated with age, $F(4,143) = 0.98$, $p = .420$.

Taken together, our results indicate that, although age was associated with increases in reaction times to incongruent stimuli in general, this effect was greater in the condition, in which the participants had to ignore the finger movement (symbolic condition) compared to the condition, in which they had to ignore the symbolic cue (movement condition).

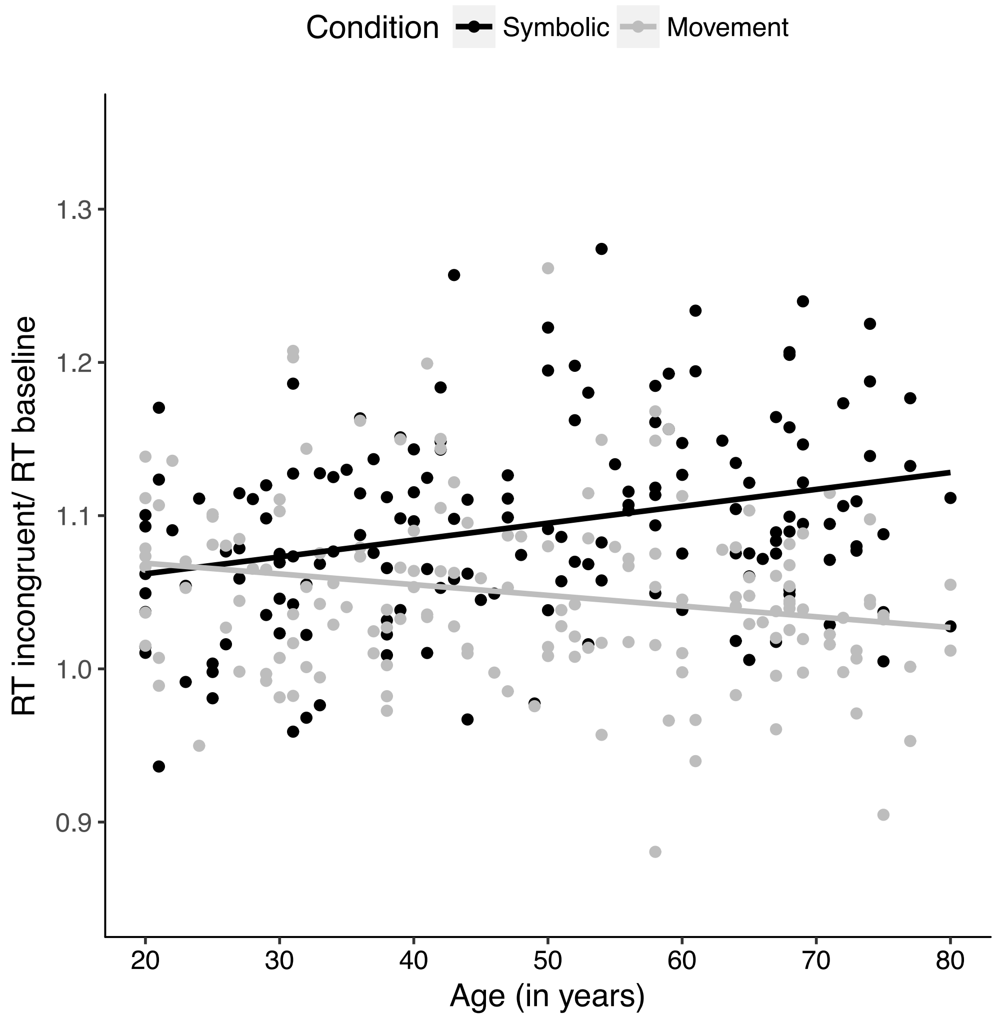

Figure 7. Regression of age (in years) on the baseline-corrected incongruent trials, separated by condition. The baseline correction was achieved by calculating the proportion of the reaction times (RTs) in the incongruent trials over the RTs in the baseline trials (e.g., a proportion of 1.1 indicates an interference of 10% in the reaction times of incongruent compared to baseline trials). See Appendix for the respective graph on congruent trials.

Discussion

In this study, we investigated age-related differences in the interrelations between action perception and action production. We explored whether advancing age influences how participants' action production is modulated by a simultaneous but incongruent action perception. Participants were asked to respond with a finger movement to the presentation of a congruent or incongruent finger movement and/or symbolic cue. Specifically, while finger movement and symbolic cue were present in all trials (except for baseline trials), participants were asked to respond either to the movement or the symbolic cue depending on the experimental condition. Participants' reaction times were longer in incongruent trials compared to congruent and baseline trials of both conditions. Within these incongruent trials, participants' action production was affected to a greater extent by the perception of an incongruent action (symbolic condition) than by the perception of an incongruent symbolic cue (movement condition). However, the older the participants were, the more pronounced this effect was. Thus, the influence of age was accentuated in the symbolic compared to the movement condition.

We partly replicated previous findings (Brass, Bekkering, et al., 2001; Brass et al., 2000) by showing that participants were slower in incongruent trials compared to congruent and baseline trials independent of age and experimental condition. However, only a subset of our participants showed shorter reaction times in congruent compared to baseline trials ($n = 28$, $M_{age} = 43.7$ years), and – on average – our participants did not show such facilitation effects. Compared to Brass et al. (2000) we substantially enlarged the sample size and included participants who differed strongly in their age. In addition to these changes in the sample characteristics, we reduced the number of trials per condition (reliability of reaction times: Cronbach $\alpha > .95$). Hence, our participants were less trained in completing the task than participants in prior studies. Therefore, it might very well be the case that the previously reported facilitation effects might show up only after a certain amount of experience with the stimuli and the task (Bertenthal et al., 2006) and are only found in more homogeneous samples.

In this study, we were primarily interested in the reaction times in incongruent trials since, for the reasons outlined in the introduction, we expected these to be influenced strongest by increasing age. The longer reaction times of our participants in incongruent compared to congruent and baseline trials indicate that the processing of two conflicting cues, the finger movement and the symbolic cue, interfered with action production (i.e., the participants' finger movement). Moreover, the increase in reaction time due to this interference was larger in the symbolic condition, in which the participants had to react to the symbolic cue and ignore the finger movement as compared to the movement condition, in which the participants were asked to react to the finger movement and ignore the symbolic cue. This is in line with the assumptions of the simulation theory (Jeannerod, 2001): In the incongruent trials of the symbolic condition in this study, action perception and production were associated with concurrent but conflicting action simulations (e.g., perception of middle-finger movement during production of index-finger movement). Hence, the associated internal action simulations might have interfered with each other leading to an increase in reaction times in incongruent trials of the symbolic condition compared to incongruent trials in the movement condition.

Alternatively, the larger difference between congruent and incongruent trials in the symbolic compared to the movement condition might be explained by low-level processes. That is, ignoring a more salient finger movement in contrast to ignoring the appearance of a symbolic cue might have been more difficult and therefore led to longer reaction times. Moreover, the reported effects might be confounded with spatial compatibility since the response finger not only matched the observed finger in terms of anatomical identity, but in terms of the side on which is was presented (right or left) and the symbolic cue was displayed on the fingernail of response finger. This is also why previous studies referred to our symbolic condition as the "spatial condition" (Brass et al., 2000). However, prior findings suggest a dissociation between imitative and spatial compatibilities, implying that they are driven by different underlying processes (Boyer, Longo, & Bertenthal, 2012; Wiggett, Hudson, Tipper, & Downing, 2011). Moreover, studies using similar paradigms have shown automatic movement imitation such as the one reported in our study independent of stimulus salience or spatial compatibility (Bertenthal et al., 2006; Catmur & Heyes, 2011; Heyes et al., 2005). Furthermore, the suppression of an incongruent movement during action perception is shown to be accompanied by increased activity of sensorimotor areas (Koski et al., 2002). Together, these findings make it unlikely that low-level processes alone explain our findings (for a review see Heyes, 2011).

In our study, advancing age was associated with the baseline-corrected incongruent trials of both experimental conditions. While it has been shown previously that increasing age is associated with a general slowing (Salthouse, 1996) and a more wide spread and less lateralized cortical activation with age (Cabeza, 2002), older adults are shown to be especially impaired when having to process several conflicting stimuli at the same time: Studies on action production during the perception of an incongruent symbolic cue report longer reaction times (Korsch et al., 2014, 2016; Maquestiaux, 2016), over-activation of brain areas involved (Zhu, Zacks, & Slade, 2010) and the activation of additional brain areas (Nielson, Langenecker, Garavan, & Hartley, 2002) for older compared to younger participants. However, these findings do not explain why the effect of age on the baseline-corrected incongruent trials is accentuated in the case action production was interfered by a simultaneous action perception (symbolic condition) compared to the condition in which action production was interfered by the simultaneous perception of a symbolic cue (movement condition).

Action production during the perception of a human action is assumed to operate on a different basis than the interference of an action-unrelated stimulus (Valchev et al., 2017). According to the simulation theory (Jeannerod, 2001), interference effects in concurrent action perception and production are mediated by the sensorimotor system. The activity of this system is shown to change with age (Sharma & Baron, 2014; Ward, 2006; Ward & Frackowiak, 2003), which is associated with a decrease of action perception (e.g., accuracy of action prediction, Diersch et al., 2012) and action production (e.g., greater movement variability and deficits in coordination, Seidler et al., 2010). Furthermore, older adults compared to younger adults show activation in additional brain areas during movement execution, coordination and action perception (Diersch et al., 2016; Heuninckx et al., 2005, 2008, 2010). As age advances, action perception and production might be increasingly associated with the activation of motor programs that are irrelevant for the on-going task. This reduced specialization might make the sensorimotor system more susceptible to challenges, which shows up as increased reaction times during simultaneous action perception and production. In line with the assumption of a less specialized processing in the sensorimotor system, older compared to younger adults show less selective corticomotor facilitation during action perception, action production and imagination (Léonard & Tremblay, 2008; Mouthon et al., 2016). Furthermore, Diersch et al. (2015) have shown an age-related decline in the distinctiveness of activation in the action-observation network (AON), a set of neuronal structures including frontoparietal regions and the posterior superior temporal sulcus (Grafton, 2009), which is active during action perception. Importantly, the age-related differences in this study were measured on the behavioural level as well and older compared to younger participants were less able to capture slight variations in the temporal continuation of a partially occluded action (also see Diersch et al., 2013, 2012). Hence, the accentuated influence of action perception on the simultaneous action production in our study might be an observable lead for age-related processes associated with a less precise internal representation and simulation of the actions perceived and produced (for a review see Costello & Bloesch, 2017). In line with this, the participants' performance in the inhibition task was not related to their motor interference. That is, the ability to inhibit an automatic response tendency was already controlled for in the motor interference score by subtracting the interference in the movement condition form the interference in the cross condition. Therefore, the motor interference score represents the influence of action perception on the simultaneous action production controlling for the effect of a second task.

Nevertheless, our results are based on the analysis of participants' behaviour. Accordingly, interpretations about the underlying physiological processes remain speculative. Future studies using TMS or imaging techniques will further explore the neural mechanisms behind the reported age-related effects in action production. Furthermore, we investigated age effects cross-sectionally. Individual differences might lead to different developmental trajectories and are better captured with longitudinal investigations.

Taken together, our findings indicate that action production is interfered by a simultaneous action perception and that this motor interference effect increases with age. Importantly, our results show that age affects action production during the perception of an incongruent action differently than action production during the perception of an incongruent symbolic cue. This indicates that the processing of perceived actions interferes with action production beyond the effect of having to process two conflicting stimuli at the same time and is especially affected by advancing age.

Study III

Higher levels of motor competence are associated with reduced interference in action perception across the lifespan

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Abstract

Action perception and action production are tightly linked and elicit bi-directional influences on each other when performed simultaneously. In this study, we investigated whether age-related differences in manual fine-motor competence and/or age affect the (interfering) influence of action production on simultaneous action perception. In a cross-sectional eye-tracking study, participants of a broad age range (N = 181, 20-80 years) observed a manual grasp-and-transport action while performing an additional motor or cognitive distractor task. Action perception was measured via participants' frequency of anticipatory gaze shifts towards the action goal. Manual fine-motor competence was assessed with the Motor Performance Series. The interference effect in action perception was greater in the motor than the cognitive distractor task. Furthermore, manual fine-motor competence and age in years were both associated with this interference. The better the participants' manual fine-motor competence and the younger they were, the smaller the interference effect. However, when both influencing factors (age and fine-motor competence) were taken into account, a model including only age-related differences in manual fine-motor competence best fit with our data. These results add to the existing literature that motor competence and its age-related differences influence the interference effects between action perception and production.

Keywords: eye tracking; action prediction; common-coding approach; motor repertoire; action production

Higher levels of motor competence are associated with reduced interference in action perception across the lifespan

Successful social interaction involves the anticipation of our interlocutor's actions (von Hofsten, 2004). This ability is assumed to be based on shared representations for perceived and produced actions (Flanagan & Johansson, 2003; Hommel et al., 2001; Prinz, 1997). Because of this common basis, action perception and production elicit bi-directional influences on each other when performed simultaneously: While concurrent and incongruent action perception and production interfere with each other, the opposite is true for concurrent and congruent perception and production (e.g., Brass, Bekkering, & Prinz, 2001). Furthermore, action perception and production are influenced by action experience (Roberts et al., 2016) and age (Diersch et al., 2012). In this study, we explored the influence of age-related differences in manual fine-motor competence on the interference effect in simultaneous action perception and production.

Previous research has shown that action perception is modulated by a concurrent action production. This results in interference effects in cases in which perceived and produced actions do not match (Jacobs & Shiffrar, 2005; Kilner et al., 2003). For instance, Hamilton, Wolpert, and Frith (2004) asked participants to lift boxes of different weights. At the same time, they were asked to make judgments about the heaviness of objects lifted by an actor. Participants perceived objects lifted by the actor to be lighter when they themselves lifted a heavy box and heavier when they lifted a light box. In the same vain, action perception is facilitated by a corresponding and simultaneously produced action (e.g., evaluation of movement durations: Hecht, Vogt, & Prinz, 2001; discrimination of hand postures: Miall et al., 2006). Similarly, action perception can facilitate (Edwards et al., 2003; Ménoret et al., 2013) or interfere with a concurrent action production (Brass, Zysset, et al., 2001; Wohlschläger & Bekkering, 2002). For example, Brass, Bekkering, and Prinz (2001) asked their participants to perform finger movements, which were either congruent or incongruent with simultaneously observed finger movements. The authors reported facilitation (i.e. shorter reaction times in participants' finger movements) in congruent trials and interference (i.e. longer reaction times) in incongruent trials.

Most commonly, these bi-directional effects are explained through a shared representational ground of perceived and produced actions ("common-coding approach"; Hommel et al., 2001). This approach assumes that similar motor programmes as those needed to produce actions are activated during action perception and planning (Gallese et al., 1996; Iacoboni et al., 1999; Léonard & Tremblay, 2008; Marty et al., 2015). In line with this, action perception and production are mediated by the activity of the sensorimotor system (Valchev et al., 2017). For instance, transcranial magnetic stimulation (TMS) applied over sensorimotor sites during action perception modulates motor corticospinal excitability in accordance with the perceived actions (Aglioti et al., 2008; Fadiga et al., 1995; Urgesi et al., 2006). Consequently, in cases in which the motor programmes activated by concurrent action perception and production differ they interfere with each other. More precisely, because the sensorimotor system is already tuned in for a certain action when producing it, the concurrent perception of a different action interferes with this movement preparation. Similarly, if the sensorimotor system is engaged in action perception, the preparation and execution of a different action interferes with the concurrent action perception (Blakemore & Frith, 2005).

In line with this view of a common representational ground for action perception and production, better abilities in producing an action go hand in hand with higher skills in perceiving that action. On the behavioural level, adults with a particular motor expertise such as figure skating (Diersch et al., 2013) or tennis (Farrow & Abernethy, 2003) predicted the correctness of a partially occluded movement continuation more precisely than novices. In the same vain, participants were more accurate in anticipating action goals when observing video recordings of their own actions than recordings of other persons' actions (Knoblich & Flach, 2001; Knoblich et al., 2002). Even a brief motor training in the respective action already enhances accuracy and speed of anticipating the action goal (Hecht et al., 2001; Möller et al., 2015). On the neural level, the activity of sensorimotor brain regions during action perception varies with the observer's previous action experience (Catmur et al., 2008, 2009; Heyes, 2010; Press et al., 2011). More specifically, the sensorimotor system shows stronger activity during the observation of actions, for which one has first-hand experience compared to actions, for which one has only observational/visual experience (e.g., dancers: Calvo-Merino et al., 2006; volleyball and tennis players: Balser et al., 2014; pianists: Haslinger et al., 2005; Haueisen & Knösche, 2001; biologically possible vs. impossible actions: Stevens et al., 2000). Taken together, these behavioural and neural studies suggest that action perception is highly dependent on the participants' level of motor expertise for the specific actions.

However, the ways we perceive actions are not only influenced by the observer's previous action experience; they are also subject to developmental change. For instance, accuracy of action anticipation (Diersch et al., 2012), imagery (Personnier et al., 2010, 2008; Saimpont et al., 2010; Skoura et al., 2005), and the perception of one's own action range (Gabbard, Caçola, & Cordova, 2011) become less precise in older adults. Of particular interest to the current study is that these age-related differences in action perception follow a similar developmental trajectory as do changes in motor competence during late adulthood (Haywood & Getchell, 2005; Houx & Jolles, 1993; Kauranen & Vanharanta, 1996). That is, increasing age is accompanied by less precise motor planning (Reuter et al., 2015) and reduced sensorimotor control of actions in older adults (Seidler & Stelmach, 1995).

Hence, in accordance with the common-coding approach (Hommel et al., 2001), one can hypothesize that the above-mentioned age-related differences in action perception (e.g., Diersch et al., 2012) are merely driven by age-related differences in motor competence and not by other age-related factors (hereinafter referred to as *age*) such as the decrease of processing speed, working memory, or inhibition (Maylor, Birak, & Schlaghecken, 2011; Park, Hedden, Davidson, Smith, & Smith, 2002). Lower levels of motor competence in later adulthood are associated with changes in the cortical representation of sensorimotor information (Karni et al., 1998; Matsuzaka et al., 2007; Poldrack et al., 2005) and less automated information processing (Rémy, Wenderoth, Lipkens, & Swinnen, 2010; Wu, Kansaku, & Hallett, 2004). These findings lead to the assumption of a higher vulnerability of the sensorimotor system to challenges such as the simultaneous processing of action perception and production. Furthermore, it can be assumed that lower levels of motor competence are associated with increased interference effects during simultaneous action perception and production, while the opposite is true for higher levels of motor competence.

In line with this, interference effects in concurrent action perception and production vary with prior active experience with specific task-related actions (Roberts et al., 2016; Capa, Marshall, & Bouquet, 2011). In the current study, we aimed to generalise these findings. The driving assumption was that action experience does not need to be task-specific to result in differences in action perception. To test this assumption, we investigated whether the participants' general fine-motor competence influences the magnitude of interference effects in simultaneous action perception and production. Specifically, our main goal was to explore whether the age-related decrease in manual fine-motor competence translates into a slower anticipation of an action goal during concurrent action production. Furthermore, we explored how this influence of manual fine-motor competence can be compared to the effect of other age-related factors – approximated by the participants' age in years.

To address these two research questions, we adapted a task from Cannon and Woodward (2008) in which participants repeatedly observed a grasp-and-transport action while performing two different distractor tasks. In a motor distractor task, the participants tapped their fingers (finger-tapping condition) and in a cognitive distractor task, they repeated a memorised sequence of letters and digits (memory condition). Crucially, in the finger-tapping condition, participants produced a motor sequence that was different from the perceived manual grasp-and-transport action. Hence, the finger-tapping condition induced unspecific noise to the sensorimotor system and this noise interfered with the simultaneous action perception. In the memory condition, no such motor interference was observed.

Using eye tracking, we assessed participants' (20–80 years) eye movements during all conditions of the above-mentioned task introduced by Cannon and Woodward (2008). As a measure of action perception, we calculated the frequency of anticipatory eye movements to the action goal (*anticipation frequency*). This measure is a well-established indicator for action perception in children and adults. Anticipatory eye movements indicate the observer's encoding of future states of the observed behaviour (Falck-Ytter et al., 2006; Gesierich et al., 2008; Melzer et al., 2012; Rosander & von Hofsten, 2011). They are present during production and perception of simple goal-directed actions (Flanagan & Johansson, 2003). Furthermore, the recruitment of the observer's motor system during action perception is causally related to anticipatory eye movements (Elsner et al., 2013). That is, anticipatory eye movements are delayed during the observation of a goal-directed action if the motor area corresponding with the effector limb of the observed action is stimulated via TMS.

In accordance with the results of the original study (Cannon & Woodward, 2008), we expected anticipation frequencies to be reduced in both distractor conditions (finger tapping and memory) compared to a baseline condition without a distractor task. In line with the original study, this reduction was expected to be greater in the finger-tapping than in the memory condition, because the production of an additional action (finger tapping) directly interferes with the perception of another action (grasp-and-transport). Based on previous studies on the development of action perception and motor competence, we expected lower levels of manual fine-motor competence and advancing age to be associated with a greater interference effect of action production onto action perception. Finally, we aimed to compare and disentangle the relative contributions of these two factors to the interference effect.

Method

Participants

We included 181 participants between the ages of 20 and 80 years (see Table 2 for a detailed description of the sample). All participants reported normal or corrected-to-normal vision. The local ethics committee approved the study and all participants gave written informed consent. Participants received a reward of CHF 30.- for their participation.

Table 2

Participants' Characteristics

Age range (years)	*N*	Gender (% female)	Handedness	Education
20-29	34	65	46.77(52.77)	4.29(1.43)
30-39	33	76	66.06(50.23)	5.55(1.54)
40-49	24	50	84.79(25.33)	5.54(1.84)
50-59	30	67	56.81(55.38)	4.77(2.00)
60-69	37	62	79.06(38.57)	4.76(2.01)
70-80	23	48	74.82(49.61)	4.70(1.66)

Note. Means and standard errors are reported for handedness and education. Handedness (in % right) was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). Highest education is reported in the range from 1 = High School to 7 = University.

Procedure

The current study is part of a larger longitudinal research project on the interrelations between action perception and action production throughout adulthood. The tasks employed in this project were designed to assess participants' oculomotor skills (e.g., smooth pursuit, saccade velocity) and their action perception operationalized via anticipatory eye movements. Furthermore, several control measures such as the participants' health status, handedness, motor or cognitive skills were included. Manual fine-motor competence and performance in the eye-tracking task were assessed in two separate lab sessions and two different rooms. The two sessions took place not more than 7 days (range: 1-7 days) apart from each other. In the eye-tracking session, the participants were seated in a dimly lit room. Prior to task instruction, the eye-tracking system and the calibration procedure were explained. Instructions for both distractor tasks were given prior to stimuli presentation and were repeated right before the actual distractor task. In the fine-motor competence session, participants were seated in front of the work plate and instructed verbally prior to each subtest.

Eye tracking

Stimuli. The stimuli consisted of a simple grasp-and-transport action, which was repeated three times in one video clip. Each clip started with an actor grasping one of three coloured balls (original size: Ø 7 cm/ 2.8 x 3.0° visual angle) on the right side of a table and transporting and dropping it into a container (original size: Ø 15 cm, height 12 cm/ 8.1 x 6.4° visual angle) on the left side of the table. This action sequence was repeated for the remaining two balls. The total duration of each video clip was 14'840 ms. The three grasping actions (from dropping the ball into the container to touching the ball) lasted 1'240 ms, 1'960 ms and 1'680 ms. The three transport actions (from touching the ball to dropping it into the container) lasted 1'960 ms, 2'080 ms and 2'200 ms.

Apparatus. Data were collected with an SR Research near-infrared eye-tracking system with a tracking rate of 500 Hz (Eyelink 1000Plus; SR Research, Canada) using the Experiment Builder Software (SR Research). Every participant was given a 9-point calibration. Stimuli were presented on a 17" display. The display and the near-infrared lights and the camera were mounted on a movable arm at a distance of 60 cm from the participant.

Design. In a within-subject design, participants repeatedly observed the described grasp-and-transport action in three different conditions (adapted from Cannon & Woodward, 2008; see Figure 8a): First, all participants watched two video sequences without a distractor task (baseline condition). Gaze behaviour during these trials served as a baseline to assess the participants’ action perception without the distraction of any additional task. Subsequently, the participants repeatedly observed the described grasp-and-transport action while performing two different distractor tasks: They either tapped their fingers (finger-tapping condition) or internally repeated a memorised sequence of letters and digits (memory condition). The order of the two latter tasks was counterbalanced between participants. In the finger-tapping condition, participants were asked to repeatedly touch their thumb successfully with every finger of their dominant hand (starting with the little or with the index finger). The order in which to tap was indicated prior to each video sequence. Participants were informed that the speed of their movement was not important, but that they should instead engage in a regular tapping rhythm. In the memory condition, one of the two sequences of digits and letters (“R6C8M”; “5L3T9”) was displayed prior to each video clip. The participants were asked to sub-vocally rehearse the sequences while watching the video clip. After two video clips, the participants were asked to verbally indicate the rehearsed sequence followed by the presentation of the second sequence. In every video a sequence of 6 action steps was shown (grasp and transport of 3 balls). Therefore, every action step was presented 12 times per baseline condition (2 video clips x 3 balls x 2 action types) and 24 times per distractor condition (2 video clips x 3 balls x 2 action types x 2 sequences). This resulted in 12 baseline trials and 24 trials for every distractor task (Figure 8a).

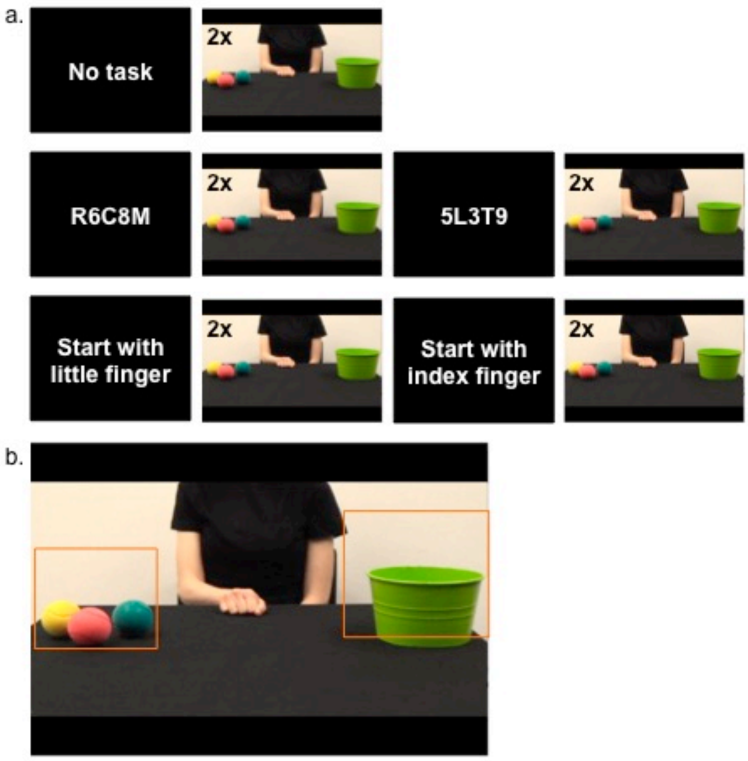

Figure 8. a. Research design with baseline, memory and finger-tapping condition. Stimulus video was shown twice per instruction. b. Still frame of stimulus video with areas of interests (AOI) covering the three balls and the container.

Data analysis. Data was reduced with the Data Viewer Software (SR Research). Two areas of interest (AOI) were defined (Figure 8b): one covering the three balls (*ball area*; 8.3 x 7.7° visual angle) and one covering the container (*container area*; 9.7 x 9.6° visual angle). For the grasping action, the ball area served as the goal AOI, and the goal area for the transport action was the container area. To ensure sufficient data quality, only trials in which participants' gaze could be assessed for at least half of the total trial duration were included. Next, the difference in time between the arrival of the actor's hand in the respective goal AOI and the participant's first fixation in the same area was calculated (gaze latency). Using this gaze latency, we calculated anticipation frequencies by dividing the number of trials in which the participants arrived prior to the actor (anticipatory gaze shifts) by the total number of trials that passed the quality criterion (anticipative and reactive gaze shifts). Since different types of actions (i.e., grasp and transport), action durations and saliencies induce unspecific variance to the data (Daum et al., 2016), anticipation frequencies as a more robust measure of action perception was used to account for this variance.

Finger tapping was coded from video. The tapping frequency was obtained by counting participants' touches of finger and thumb and dividing this number by the duration of the two videos (2 * 14.840 s). Performance in the memory condition was measured via the number of sequences remembered correctly and ranged from 0 to 2.

Manual fine-motor competence

As a measure of the participants' general level of manual fine-motor competence, we assessed their fine-motor skills with subtests of the Motor Performance Series (*Motorische Leistungsserie*, MLS; Neuwirth & Benesch, 2011). The computer-based test-battery consists of a work plate with a separate pencil for each hand. Four subtests were included, for which age norms were available for participants between 20 and 80 years (Sturm & Büssig, 1985), and which have been used in previous studies with older participants (e.g., Binder et al., 2016). The selected subtests measure the ability to hold a steady arm-hand position (subtest *steadiness*), the speed and accuracy of slow (*lines*) and fast (*aiming*) arm-hand movements, and the accuracy and speed of fast wrist-finger movements (*tapping*). Time and number of errors were assessed for every subtask. A composite score of all subtests (according to Platz, Prass, Denzler, & Bock, 1999) was calculated for the dominant hand – as assessed by the handedness test (Oldfield, 1971). The scale of this motor competence score is inverted: The more negative the individual score, the better the participant's manual fine-motor competence.

Results

There were no effects of order of condition ($p = .91$) or action type ($p = .23$). Therefore, we collapsed the data across the two orders and action types for all further analysis. On average, sufficient gaze data was obtained for $M = 93.42\%$ ($SD = 8.36\%$) of all trials presented in the baseline condition, for $M = 87.66\%$ ($SD = 13.38\%$) of all trials in the finger-tapping condition, and for $M = 89.82\%$ ($SD = 13.21\%$) of all trials in the memory condition. The number of trials for which sufficient gaze data was obtained did not differ between the two distractor conditions ($p = .25$). However, slightly more trials were included in further analyses in the baseline condition compared to the two distractor conditions ($p < .001$).

We measured participants' performance in the two distractor conditions to make sure that they followed the task instructions. On average, participants engaged in a tapping frequency of $M = 1.97$ touches per second ($SD = 0.68$). Participants with a high tapping frequency in action production also showed a high anticipation frequency in action perception during the finger-tapping condition, $r = .24$, $p = .002$. This makes it unlikely that lower anticipation scores in action perception occurred because participants were shifting their attention from action perception to action production. In the memory condition, participants remembered $M = 1.83$ ($SD = 0.43$) sequences correctly. The number of sequences remembered did not correlate with the anticipation frequency in the memory condition, $r = -.02$, $p = .79$. The subsequent analyses are divided into two sections. To replicate previous findings, we compared the raw scores of the anticipation frequencies in all three experimental conditions (baseline, memory and finger tapping). Next, the contributions of age-related differences in manual fine-motor competence and other age-related factors to this result pattern were explored using the difference scores between the baseline condition and the two distractor conditions (see Table 3 for descriptive statistics on the reliability of measures).

Table 3

Correlation and Reliability of Raw Scores and Difference Scores

	1	2	3	4	5	6	7	*Mean(SD)*	Reliability
(1) Frequency baseline	-	0.30***	0.41***	0.43***	0.41***	0.16*	0.24**	67.89(18.61)	0.52
(2) Frequency finger tapping	0.30***	-	0.55***	-0.73***	-0.31***	-0.26***	-0.10	48.82(24.75)	0.86
(3) Frequency memory	0.41***	0.55***	-	-0.23**	-0.66***	-0.11	0.06	63.43(22.56)	0.79
(4) Interference finger tapping	0.43***	-0.73***	-0.23**	-	0.59***	0.36***	0.26***	19.07(26.17)	0.87
(5) Interference memory	0.41***	-0.31***	-0.66***	0.59***	-	0.24**	0.13	4.46(22.61)	0.79
(6) Motor competence	0.16*	-0.26***	-0.11	0.36***	0.24**	-	0.48***	-1354.14(622.43)	-
(7) Age	0.24**	-0.10	0.06	0.26***	0.13	0.48***	-	-	-

Note. Zero-order correlations of variables of interest (*** p < 0.001; ** p < 0.01; * p < 0.05). Mean and standard deviation of anticipation frequencies are reported in percentage of trials anticipated (number of trials anticipated per number of trials for which sufficient gaze data could be obtained). Reliability scores refer to Spearman-Brown corrected split-half reliability. Reliability scores for motor competence are not reported because the respective subtests only involved one trial.

Interference effect

First, we explored whether performing a distractor task interfered with the simultaneous anticipation of the action goal, resulting in reduced anticipation frequencies for the two distractor conditions (finger tapping or memory) compared to the baseline condition. A repeated measures ANOVA with a Greenhouse-Geisser correction determined that the mean anticipation frequency differed between the three conditions, $F(2,360) = 63.571$, $p < .001$, $\eta^2 = .120$. Post-hoc tests using Bonferroni correction revealed that anticipation frequencies were lower in both distractor conditions (finger-tapping condition: $M = 48.83$, $SD = 24.75$; memory condition: $M = 63.43$, $SD = 22.57$) than in the baseline condition ($M = 67.90$, $SD = 18.61$; finger-tapping condition: $p < .001$; memory condition: $p = .026$). Furthermore, the anticipation frequency in the finger-tapping condition was lower than in the memory condition, $p < .001$ (Figure 9).

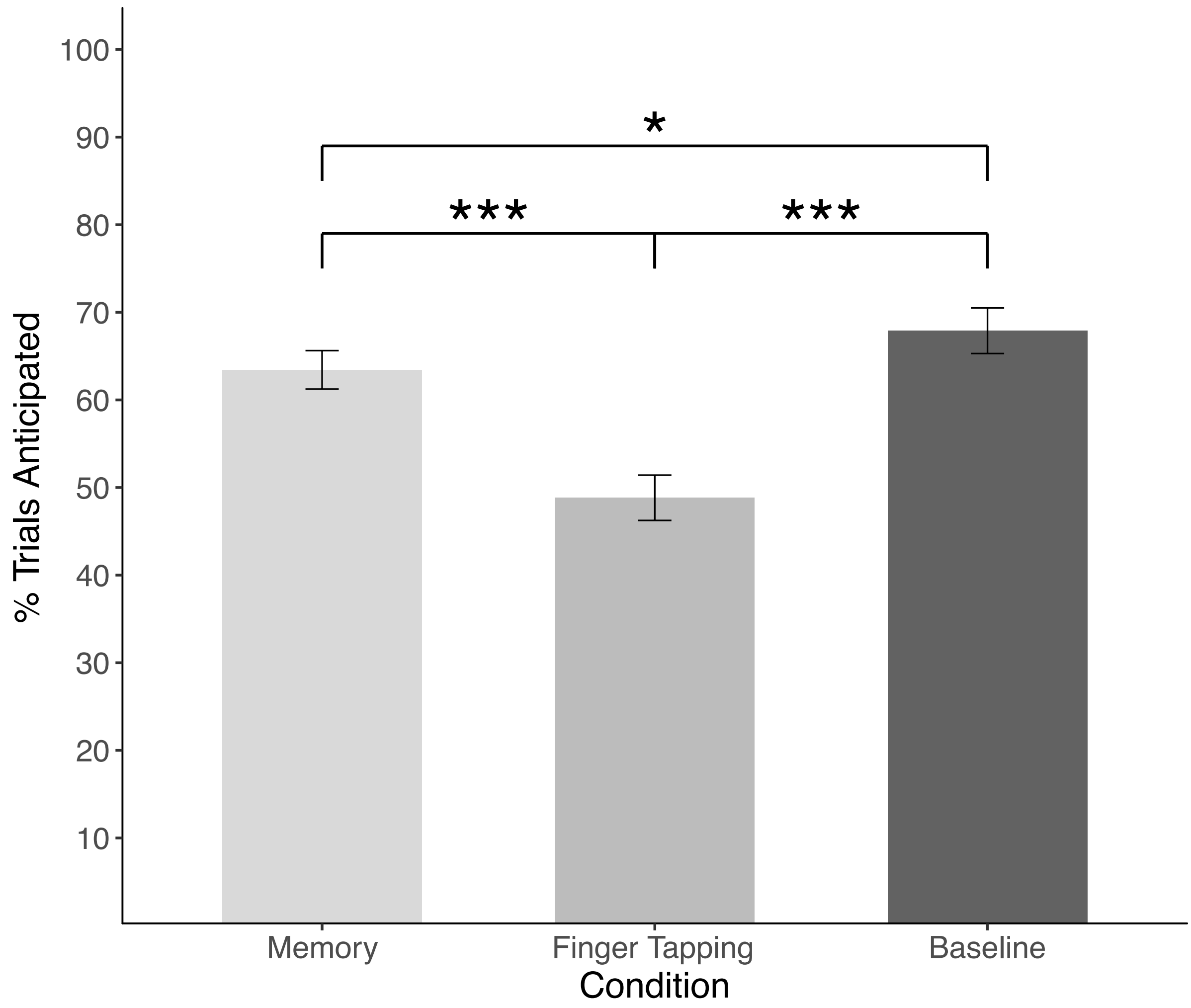

Figure 9. Percentage of trials anticipated (anticipation frequency) per experimental condition (* $p < .05$; *** $p < .001$).

Influence of manual fine-motor competence and age on interference effect

Next, we assessed the effects of manual fine-motor competence and age on the interference in action perception in the two distractor conditions. For this, we first calculated separate interference scores for each distractor condition by subtracting the anticipation frequency in the respective distractor condition from the anticipation frequency in the baseline condition. Using R (R Core Team, 2012) and lme4 (Bates, Maechler, Bolker, & Walker, 2015) we performed linear mixed effects analyses, building all subsequent models on a baseline model (Model 1). This model investigated the effect of distractor condition on the interference score. The model included the two distractor conditions (finger-tapping condition and memory condition) as fixed effects and the intercepts for the subjects as random effects (see Table 3 for model overview).

Age. To analyse the extent to which age moderates the effect of distractor condition on the interference effect, we added age and its interaction with distractor condition as fixed effects (Model 2) and compared this model to the baseline model (Model 1). Model 2 provided a better fit with the data than Model 1 (see fit indices in Table 5). This suggests that age moderates the effect of distractor condition on the interference in action perception (Table 4). To further analyse the effects of age in the two experimental conditions, we conducted two separate linear regressions of age on the interference effects for both distractor conditions. Age was only associated with the interference effect in the finger-tapping condition, $F(1,179) = 13.51$, $p < .001$, $R^2 = .070$, but not in the memory condition, $F(1,179) = 3.26$, $p = .073$.

Manual fine-motor competence. We investigated the extent to which manual fine-motor competence moderates the effect of distractor condition on the interference score by adding participants' motor competence score and its interaction with distractor condition as fixed effects (Model 3). Model 3 provided a better fit with the data than Model 1 and Model 2 (Table 5). This suggests that manual fine-motor competence moderates the effect of distractor condition on the interference in action perception (Table 4). To explore the effect of manual fine-motor competence in the experimental conditions in more detail, we conducted separate linear regressions of participants' motor competence score on the interference effects in both distractor conditions. Manual fine-motor competence was significantly associated with the interference effect in the finger-tapping condition, $F(1,177) = 26.56$, $p < .001$, and in the memory condition, $F(1,177) = 10.52$, $p = .001$. However, the effect was greater in the finger-tapping condition, $R^2 = .131$ than in the memory condition, $R^2 = .056$ (Figure 10).

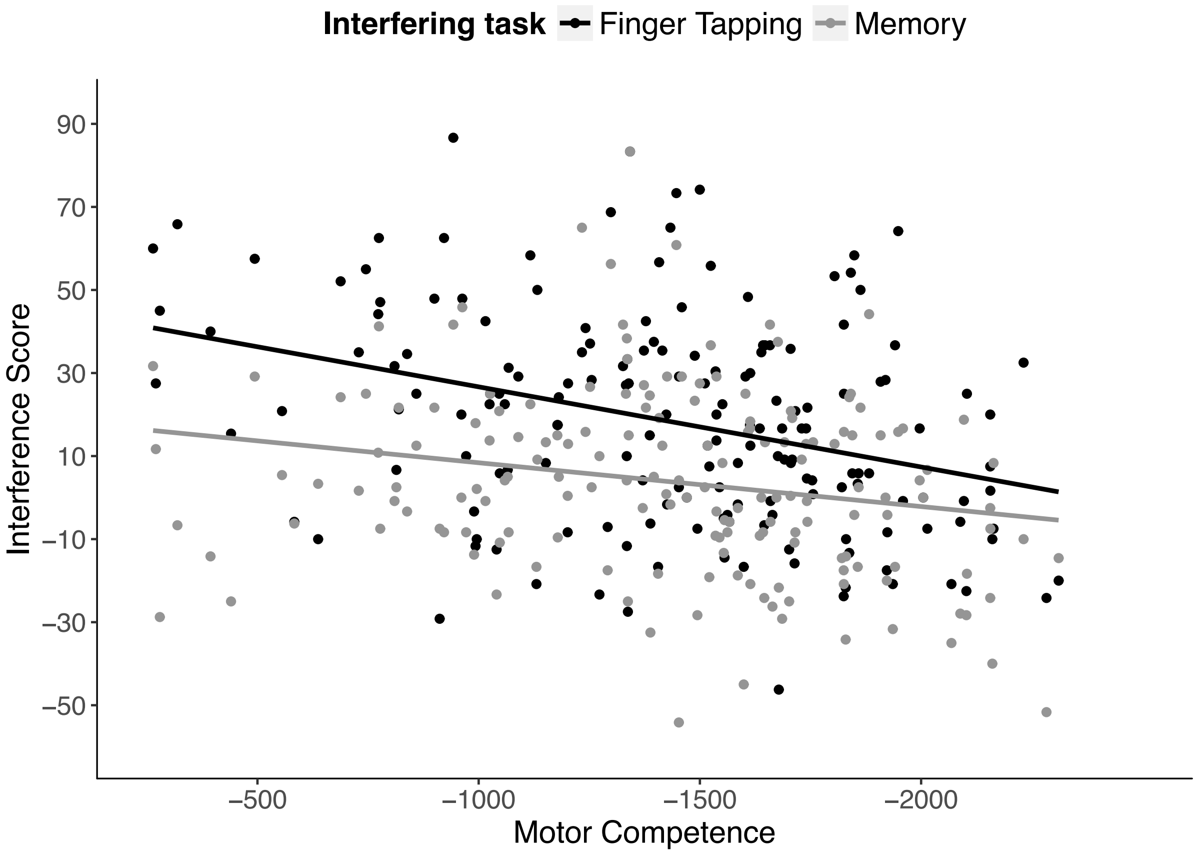

Figure 10. Relationship between manual fine-motor competence and interference score in both distractor conditions. Note that lower motor competence scores reflect better manual fine-motor competence.

Age and manual fine-motor competence. To explore the extent to which age and manual fine-motor competence together moderate the effect of distractor condition on the interference score, we compared a full model (Model 4) with the baseline model (Model 1). In the full model, age and its interaction with distractor condition, and participants' motor competence score and its interaction with distractor condition were added as fixed effects. Model 4 provided a better fit with the data than Model 1 (Table 5). When comparing the full model (Model 4) with the Models 2 and 3, Model 4 fit the data better than Model 2. However, it did not provide a better fit with the data than the more parsimonious Model 3. This suggests that Model 3 provided the best fit with the data. Our results therefore indicate that age-related differences in manual fine-motor competence – without taking other age-related factors into account –moderate the effect of the distractor condition on the interference in action perception (Table 4).

Table 4

Linear Mixed Models

Coefficient		Estimate	*SD*	*p*
	Model 1			
Fixed parameters	Constant	0.191	0.018	
	Condition	-0.146	0.017	<.001
Random parameters	Subjects	0.034	0.185	
	Model 2			
Fixed parameters	Constant	0.013	0.052	
	Condition	-0.039	0.049	<.001
	Age	0.004	0.001	.004
	Age * Condition	-0.002	0.001	.020
Random parameters	Subjects	0.033	0.180	
	Model 3			
Fixed parameters	Constant	0.965	0.042	
	Condition	-0.235	0.040	<.001
	Motor competence	0.000	0.000	<.001
	Motor competence * Condition	0.000	0.000	.014
Random parameters	Subjects	0.029	0.171	
	Model 4			
Fixed parameters	Constant	0.299	0.086	
	Condition	-0.140	0.082	<.001
	Age	0.001	0.001	.453
	Age * Condition	-0.001	0.001	<.001
	Motor competence	0.000	0.000	.184
	Motor competence * Condition	0.000	0.000	.129
Random parameters	Subjects	0.029	0.171	

Note. Model 1 explores the effect of distractor condition (Condition) on the interference score. Model 2 investigates the extent to which age moderates the effect of distractor condition. Model 3 investigates the extent to which motor competence moderates the effect of distractor condition and Model 4 explores the effects of age and motor competence on the interference effects within one model.

Table 5

Fit Indices and Model Comparison

	Df	AIC	BIC	Log likelihood
Model 1	4	-59.375	-43.853	33.688
Model 2	6	-68.892	-45.609	40.446
Model 3	6	-83.530	-60.246	47.765
Model 4	8	-81.886	-50.842	48.943

Discussion

In the present study, we investigated how the relationship between action perception and action production differs throughout adulthood and how manual fine-motor competence is related to these differences. We used an interference paradigm to assess how the anticipation of an action goal (as a means of assessing action perception) is influenced by simultaneous action production. Furthermore, we were interested in whether and how this influence varies with the observer's manual fine-motor competence and/or age. The findings show that participants throughout the adult life span, from 20 to 80 years, anticipated the goal of a grasp-and-transport action less often when they simultaneously performed finger-tapping movements or mentally rehearsed a sequence of numbers and letters. This interference was strongest with a concurrently performed action. Furthermore, the interference effect increased with participants' advancing age and decreased with participants' increasing manual fine-motor competence. Importantly, manual fine-motor competence elicited a stronger influence on the interference effect in the finger-tapping compared to the memory condition. Moreover, a model including only age-related differences in manual fine-motor competence fit the data better than a model including both fine-motor competence and other age-related factors.

Our results are in line with previously reported interference effects of action perception on action production and vice versa (e.g., Catmur, 2016; Hamilton et al., 2004; Kilner et al., 2003; Press et al., 2008). Importantly, the memory condition did interfere with action perception less strongly than the finger-tapping condition: Producing an action while simultaneously perceiving a different action was more challenging than mentally rehearsing a sequence of letters and digits during action observation. That is, although both conditions involved the simultaneous processing of two tasks, they resulted in different effects. Therefore, the reduction in the anticipation frequency in the finger-tapping condition cannot solely be explained by a mere dual-task effect. Hence, there seems to be something uniquely related to the interference in the finger-tapping condition: According to the principle of common-coding, perceived, and produced actions are represented in a shared domain, and overlapping resources are assumed to account for perceiving, imagining, representing, planning, and executing actions (Hommel et al., 2001; Prinz, 1990, 1997). During simultaneous perception and production of two different actions, therefore, two different motor representations are active and simultaneously require cognitive and sensorimotor resources. This results in the reported interference effects.

In our study, the participants' level of manual fine-motor competence influenced the magnitude of interference of action production on the simultaneous action anticipation. This is consistent with previous research on the effects of motor expertise (Calvo-Merino et al., 2006; Diersch et al., 2012) and training (Möller et al., 2015) on action perception and on the interrelations of action perception and production (Capa et al., 2011; Roberts et al., 2016). Our results extend these findings, suggesting that not only motor expertise with a specific task-relevant action, but the more general level of motor competence can affect action perception. In line with this view, participants' manual fine-motor competence influenced their anticipation of the action goal in both distractor tasks. This suggests that different levels of manual fine-motor competence not only shape the participants' action production but also their general ability to anticipate an observed action goal. A simultaneously executed second task interferes with action anticipation, and the more this second task involves the sensorimotor system, the stronger this interference becomes.

In line with previous research (Diersch et al., 2013; Personnier et al., 2010, 2008), our results indicate that the participants' age accounts for some variance in the interference effect between action perception and production. However, in contrast to prior studies, our results suggest that the participants' age-related differences in manual fine-motor competence explain the interference effect better than age in years. Previous studies reporting age differences in action perception often failed to measure the participants' general level of motor competence (e.g., Gabbard et al., 2011). In light of the present results, their findings could be reinterpreted: For example, when evaluating walking distances, older participants reported the walking goal to be further away than younger participants (Sugovic & Witt, 2013). However, not age per se but the participants' own (age-related) walking ability might have influenced their perception of the walking distance. In accordance with this view, in young adults' action planning is influenced by their fitness and the amount of effort they have to put into action production (Jacobs & Shiffrar, 2005). For instance, young participants perceived hills to be steeper when they were tired or out of shape. In this case, their judgments of the steepness of the hill slopes was comparable to those of older adults (Bhalla & Proffitt, 1999). Accordingly, the current state of motor competence substantially impacts the perception of the environment with which to interact.

In our sample, participants' age was significantly associated with their level of manual fine-motor competence ($r = 0.48$, $p < .001$). This is in line with previous research showing a decrease of motor competence with advancing age (Haywood & Getchell, 2005; Kauranen & Vanharanta, 1996). Importantly, a model including only manual fine-motor competence as a predictor of anticipation frequency yielded a better fit with the data than a model with both age and manual fine-motor competence included as predictors. Therefore, our findings suggest that the observer's chronological age does not influence the anticipation of an action goal independently of his or her level of manual fine-motor competence. We assume that high levels of motor competence enable motor information to be processed in a more automated and efficient manner (Poldrack et al., 2005; Rémy et al., 2010; Wu et al., 2004). This results in the sensorimotor system being more robust against stressors such as an interfering distractor task or age-related de-differentiation processes. In line with this notion, action perception does not interfere with simultaneous action production if the action is highly automated (Hardwick & Edwards, 2012). Furthermore, increasing age goes hand in hand with slower automatization of trained actions (Wu & Hallett, 2005), while effects of age on action perception and production are reduced in participants with high task-related motor expertise (Diersch et al., 2013; Krampe, 2002; Schorer & Baker, 2015). Our findings add to this research by associating the more general level of manual fine-motor competence with an increased resistance against interference of a concurrently performed action on the anticipation of action goals.

One issue of the current study, which has to be treated with caution, is the separation of age as an assessment of other age-related factors (such as working memory or attention) and manual fine-motor competence. Specifically, like most assessments of motor competence, the Motor Performance Series (MLS) measures attentional and cognitive processes as well. For the following reasons, it is nevertheless reasonable to conclude that our participants' MLS score is largely determined by their fine-motor skills and only to a small part by other cognitive or attentional factors: First, the MLS shows divergent validity to common cognitive tests (i.e., HAWIE, CFT, STROOP; r_{max} = .35; Neuwirth & Benesch, 2011) and convergent validity to other indicators of motor competence. For example, the MLS discriminates between motor novices and experts (Kattenstroth, Kolankowska, Kalisch, & Dinse, 2010). In addition, participants' performance in the MLS battery correlates with their resting state sensorimotor connectivity (Seidler et al., 2015) and their grey and white matter volume in the primary motor cortex (Koppelmans et al., 2015). Second, our sum score of manual fine-motor competence combines both accuracy and speed measures and therefore accounts for the speed-accuracy trade-off often associated with advancing age (Forstmann et al., 2011).

In this study, we replicated and extended previous findings (Cannon & Woodward, 2008) across a broad age range. The use of eye-tracking technology and anticipatory gaze shifts as an online measure of action perception is a promising route for further research since it allows the use of comparable measurement techniques across the whole lifespan, from infancy to old age. Furthermore and in particular, longitudinal research is needed to answer open questions such as whether action perception and production follow similar developmental trajectories. Eventually, this might lead to a research-driven developmental theory on the stability and change of the interrelation between action perception and production (Loeffler et al., 2016).

Taken together and extending prior work, our results support a common processing system for action perception and production. They furthermore suggest that the general level of motor competence affects action perception similarly across a large age range. That is, independent of the level of manual fine-motor competence, age had no additional effect on the interference between action perception and production. These findings lay an additional cornerstone in understanding the interrelations between action perception and production across the whole lifespan.

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Appendix A: Additional figures and tables

Table A1

Study I. Correlations among Variables of Interest

	1	2	3	4	5	6	7
Age (1)	-	.059	.101	.038	.253**	.147	.252**
Anticipation frequency, familiar (2)	.059	-	.263**	.061	-	-	-
Recurrence, familiar (3)	.101	.263**	-	.000	-	-	-
Imitation score, familiar (4)	.038	.061	.000	-	-	-	-
Anticipation frequency, unfamiliar (5)	.253**	-	-	-	-	.224*	.086
Recurrence, unfamiliar(6)	.147	-	-	-	.224*	-	.090
Imitation score, unfamiliar (7)	.252**	-	-	-	.086	.090	-

Note. Zero-order correlations of variables of interest (** $p < 0.01$; * $p < 0.05$). Please note that anticipation frequencies, recurrence rate and imitation scores for familiar and unfamiliar actions were derived from two different age-matched samples.

Table A2

Study I. Regression Analyses: Age on Imitation Score

Model	β	*SE*	ΔR^2	*p*
	Familiar condition			
Linear Model			.144	< .001
Constant	12.637	0.319		< .001
Age	0.056	0.013		< .001
Quadratic Model			.332	< .001
Constant	14.573	0.459		< .001
Age	0.079	0.013		< .001
Age^2	-0.003	0.001		< .001
	Unfamiliar condition			
Linear Model			.063	.010
Constant	10.601	0.300		< .001
Age	0.033	0.013		.010
Quadratic Model			.220	< .001
Constant	12.133	0.434		< .001
Age	0.052	0.012		< .001
Age^2	-0.003	0.001		< .001

Table A3

Study I. Regression Analyses: Age on Measures of Action Perception

Model	β	*SE*	ΔR^2	*p*	β	*SE*	ΔR^2	*p*
	Familiar condition							
	Anticipation frequency				Recurrence rate			
Linear Model			.003	.549			.010	.300
Constant	0.572	0.017		< .001	0.060	0.000		< .001
Age	0.000	0.000		.549	0.000	0.000		.300
Quadratic Model			.009	.615			.010	.590
Constant	0.589	0.027		< .001	0.060	0.004		< .001
Age	0.000	0.000		.407	0.000	0.000		.330
Age^2	-0.000	0.000		.434	-0.000	0.000		.990
	Unfamiliar condition							
	Anticipation frequency				Recurrence rate			
Linear Model			.064	.009			.022	.130
Constant	0.496	0.016		< .001	0.057	0.003		< .001
Age	0.002	0.001		.009	0.000	0.000		.130
Quadratic Model			.084	.010			.102	.004
Constant	0.527	0.025		< .001	0.068	0.005		< .001
Age	0.002	0.000		.003	0.000	0.000		.014
Age^2	-0.000	0.000		.129	-0.000	0.000		.003

Table A4

Study I. Regression Analyses: Imitation Score on Measures of Action Perception

Model	β	*SE*	ΔR^2	*p*	β	*SE*	ΔR^2	*p*
	Familiar condition							
	Anticipation frequency				Recurrence rate			
Model			.006	.890			.035	.311
Constant	0.570	0.018		< .001	0.058	0.003		< .001
Age	0.000	0.001		.777	0.000	0.000		.154
Imitation	0.003	0.006		.549	0.000	0.001		.958
Age * Imitation	0.000	0.000		.667	0.000	0.000		.182
	Unfamiliar condition							
	Anticipation frequency				Recurrence rate			
Model			.076	.046			.193	< .001
Constant	0.491	0.017		< .001	0.072	0.005		< .001
Age	0.002	0.001		.008	0.000	0.000		.010
Age^2	-	-		-	-0.000	0.000		< .001
Imitation	0.001	0.005		.848	-0.003	0.001		.041
Age * Imitation	0.000	0.000		.750	-0.000	0.000		.055
Age^2 * Imitation	-	-		-	0.000	0.000		.814

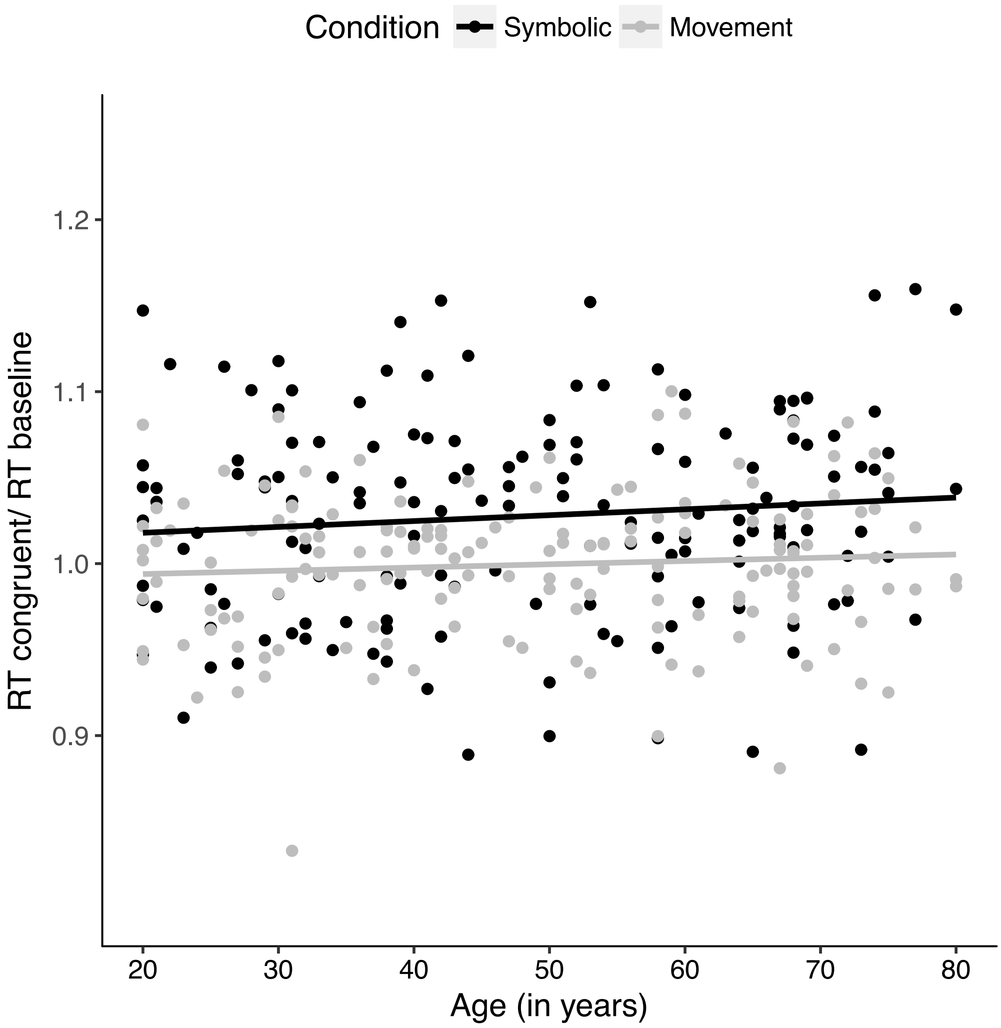

Figure A1. Study II. Regression of age (in years) on the baseline-corrected congruent trials, separated by condition.

Appendix B: List of figures

Appendix C: List of tables

Curriculum Vitae

Stephanie Wermelinger

23.03.1989

Education

02/2015 – currently	**PhD studies in Developmental Psychology** University of Zurich, Zurich Switzerland Project: „The interrelations of action perception and action production across the life span“ Supervisor: Prof. Dr. Moritz M. Daum
02/2015 – currently	**PhD program, International Max Planck Research School** “The Life Course: Evolutionary and Ontogenetic Dynamics” A joint international PhD program with the Max Planck Institute for Human Development, the Freie Universität Berlin, the Humboldt-Universität zu Berlin, the University of Michigan, the University of Virginia, and the University of Zurich.
02/2013 – 01/2015	**Master of Science in Psychology** Cognitive Psychology and Cognitive Neuroscience University of Zurich, Zurich, Switzerland Thesis: „Kommunikationsreparatur mono- und bilingualer Kleinkinder“ [Communication repair of mono- and bilingual toddlers] Supervisor: Dr. Anja Gampe
08/2009 – 01/2013	**Bachelor of Science in Psychology** University of Zurich, Zurich, Switzerland Thesis: „Stress-protektive Faktoren in der Schwangerschaft“ [Stress-protective factors in pregnancy] Supervisor: Dr. Pearl Ghaemmaghami
08/2008 – 07/2009	**Studies of Human Medicine** University of Zurich, Zurich, Switzerland

Professional Experience

08/2014 – 01/2015 **Student assistant** (Supervisor: Prof. Dr. Elke Hildebrandt)
School of Education, Chair for Teaching, Development at Pre-Primary and Primary School Level, University of Applied Sciences Northwestern Switzerland, Windisch, Switzerland

08/2011 – 02/2012 **Student assistant** (Supervisor: lic. phil. Debbie Mandel)
Department of Educational Sciences, University of Zurich, Zurich, Switzerland

Publications for peer-reviewed scientific journals

Wermelinger, S., Gampe, A., Behr, J., & Daum, M. M. (2017). Interference of action perception on action production increases across the adult life-span. *Experimental Brain Research.* doi: 10.1007/s00221-017-5157-3.

Wermelinger, S., Gampe, A., & Daum, M. M. (2017). Higher levels of motor competence are associated with reduced interference in action perception across the lifespan. *Psychological Research*, *1-13*. doi: 10.1007/s00426-017-0941-z

Wermelinger, S., Gampe, A., & Daum, M. M. (2017). Bilingual toddlers have advanced abilities to repair communication failure. *Journal of Experimental Child Psychology*, *155*, 84-94. doi:10.1016/j.jecp.2016.11.005

Oral contributions

Talks

Wermelinger, S. (2017). Associations between action production and action perception across the life span. Talk presented at the LIFE Fall Academy, University of Zurich, Zurich, Switzerland.

Wermelinger, S. (2017). Interference in action production across the adult life-span. Talk presented at PAEPSY, Münster, Germany.

Wermelinger, S. (2016). Interferenzeffekte in Handlungswahrnehmung und –produktion [Interference effects in action perception and action production]. Talk presented at 50. Kongress der Deutschen Gesellschaft für Psychologie. Leipzig, Germany.

Wermelinger, S. (2016). If what you see is not what you do. Interference effects between action perception and production across the life-span. Talk presented at the LIFE Fall Academy, MPI for Human Development, Berlin, Germany.

Posters

Wermelinger, S., Ferreira-Cunha, V.,Gampe, A., & Daum, M. M. (2017). Children reduce their communicative behaviour appropriately. Poster presented at 14th International Congress for the Study of Child Language, Lyon, France.

Wermelinger, S., Gampe, A., & Daum, M. M. (2017). Interference between action perception and action production across the adult life-span. Poster presented at Aging and Cognition, UZH, Zurich, Switzerland.

Wermelinger, S., Gampe, A., & Daum, M. M. (2016). Perceiving others' actions: Action simulation across the adult life span. Poster presented at the LIFE Spring Academy, UVA, Charlottesville, Virgina, USA.

Wermelinger, S., Gampe, A., & Daum, M.M. (2016). Bilingual Toddlers have Advanced Abilities to Repair Misunderstandings. Poster presented at International Congress on Infant Studies. New Orleans, USA.

Wermelinger, S., & Daum, M. M. (2015). The interrelations of action percption and action production across the lifespan. Poster presented at the LIFE Fall Academy, Schloss Marbach, Germany.

Gampe, A., Grassmann, G., Wermelinger, S., & Daum, M. M. (2015). Bilingual children's communicative advantage in repairing a misunderstanding. Poster presented at 2015 SRCD Biennial Meeting, Philadelphia, Pennsylvania, USA.

Outreach activities

Publications for the public

Wermelinger, S. (2017). Growing up with two languages. How this shapes toddlers' communication skills [Blog post]. Retrieved from http://bold.expert/growing-up-with-two-languages/

Media coverage

Magdalena Seebauer (2017, April 28). Zweisprachige Kinder klären Missverständnisse. [Bilingual toddlers repair misunderstandings.] Article appearing in *Der Landbote*, *Freiburger Nachrichten*, *Luzerner Zeitung*, *Südostschweiz*, *Unterländer*

beziehungsweise (2017, April). Wussten Sie, dass Zweisprachigkeit auch andere kommunikative Fähigkeiten von Kleinkindern erhöht? [Did you know that bilingualism increases communicative skills in toddlers?]

Spiegel Online (2017, February 2). Zweisprachige Kinder klären Irrtümer eher auf. [Bilingual children are more likely to repair misunderstandings.] Retrieved from http://www.spiegel.de/gesundheit/psychologie/zweisprachige-kinder-klaeren-irrtuemer-eher-auf-a-1134674.html

Peer mentoring

Member of peer mentoring group *Real Life Health Measurement (RLHM)*

Supervision of students

Master theses

Fall 2017	**Christina Herzog:** Entwicklung vom Handlungsverständnis. [The development of action understanding.]
	Vanessa Ferreira Cunha: Kommunikative Adaptionsfähigkeit mono- und bilingualer Kinder an unterschiedliche Gesprächspartner. [Communicative adaption of mono- and bilingual children to different interaction partners.]
Spring 2017	**Janni Behr**: Der Zusammenhang von Wahrnehmung und Handlung über die Lebensspanne: Erhöhte Interferenzeffekte durch die Wahrnehmung. [The interrelations of action perception and action production across the life span: Accentuated interference effects through action perception.]

Bachelor theses

Fall 2017	**Annamária Júlia Hardmeier:** Bilingualismus und Bikulturalität: Unterschiedliche Einflüsse auf die Entwicklung von exekutiven Funktionen bei bilingualen Kindern? [Bilingualism and biculturality: Different influences on the development of executive functions in bilingual children?]
Fall 2016	**Brigitte Hauser Chartouni**: Die Entwicklung der Visual Word Form Area von der Kindheit bis ins Erwachsenenalter. [The development of the Visual Word Form Area from childhood to adulthood.]
Spring 2016	**Evelyn Fuentes**: Bilingualismus und exekutive Funktionen bei Kindern – eine Übersichtsarbeit. [Bilingualism and executive functions in children – a review.]

Interns

02/2015 – 08/2017	Jannis Behr, Jean Bernardsgrütter, Ingo Besserdich, Gaja Furrer, Vanessa Meili, Jan Nussbaumer

Academic teaching

Spring 2017	**Bachelor seminar**. Social-cognitive development. Psychology, University of Zurich
Fall 2017	**Master seminar**. Social and emotional development during childhood, Psychology, University of Zurich
Spring 2016	**Bachelor seminar**. Social-cognitive development. Psychology, University of Zurich
Fall 2016	**Master seminar**. Social-emotional development during childhood, Psychology, University of Zurich

Prizes and awards

04/2016	**Recipient of travel grant** for attending the International Congress of Infant Studies in New Orleans (U.S.), funded by the Department of Psychology at the University of Zurich, CHF 1255.-
03/2016	**Recipient of grant** for hiring a research assistants for the project "The Interrelations of Action Perception and Action Production Across the Adult Lifespan.", funded by the Jacobs Foundation, CHF 8004.-